Migrate, defend, and evolve: Theoretical ecology presented in three different ways

Migrieren, Verteidigen, Evolvieren: Dreierlei der theoretischen Ökologie
Zur Erlangung des Grades eines Doktors der Naturwissenschaften (Dr. rer. nat.)
genehmigte Dissertation von Tatjana Isabell Thiel aus Offenbach am Main
Tag der Einreichung: 20.05.2019, Tag der Prüfung: 08.07.2019
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1. Gutachten: Prof. Dr. Barbara Drossel
2. Gutachten: Prof. Dr. Nico Blüthgen

TECHNISCHE UNIVERSITÄT DARMSTADT

Fachbereich Physik
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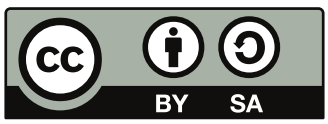

Erklärung zur Dissertation

Hiermit versichere ich, die vorliegende Dissertation ohne Hilfe Dritter nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben. Alle Stellen, die aus Quellen entnommen wurden, sind als solche kenntlich gemacht. Diese Arbeit hat in gleicher oder ähnlicher Form noch keiner Prüfungsbehörde vorgelegen.

Darmstadt, den 24.07.2019

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(Tatjana Thiel)

Zusammenfassung

Ökosysteme sind ständigem Wandel ausgesetzt. Durch den menschlichen Einfluss beschleunigen sich viele dieser Änderungen, wie der Klimawandel oder die Immigrationsrate invasiver Spezies. Die Menschheit ist daran interessiert, dass das Ökosystem, in dem sie lebt und deren Teil sie ist, stabil bleibt unter derartigen Einflüssen. In der Tat konnten schon einige Eigenschaften von Spezies identifiziert werden, die die Stabilität von Ökosystemen beeinflussen können. Da sich diese durch evolutionäre Anpassung an die herrschenden Bedingungen verändern können, ist es vor allem auch wichtig zu verstehen unter welchen Bedingungen solche Eigenschaften für die ausprägende Spezies von Vorteil sind.

In dieser Thesis analysieren wir drei Eigenschaften von Spezies, die die Stabilität von Ökosystemen beeinflussen können, nämlich die Verteidigung von Beute gegen Prädatoren, die Migration von Spezies zwischen Habitaten und die intraspezifische Merkmalvariabilität von Pflanzen. Genauer gesagt betrachten wir reservoir-basierte Verteidigung, das heißt die Beute besitzt ein Sekretreservoir, das mit der Zeit biosynthetisch aufgefüllt wird. Die Beute nutzt eine gewisse Sekretmenge für die Verteidigung gegen eine Prädatorenattacke und ist nicht verzehrbar solange sie diese Menge zur Verfügung hat. Bei der Migration von Spezies werden wir uns auf kleine Migrationsraten konzentrieren, für die stochastische Effekte relevant werden, d.h. wir betrachten die sogenannte stochastische Migration. Schlussendlich berücksichtigen wir, dass sich Pflanzenindividuen innerhalb einer Spezies, aber auch Pflanzenteile eines Pflanzenindividuums stark in ihren Merkmalen unterscheiden können und untersuchen den Einfluss dieser Variabilität auf Herbivoren. Einen besonderen Blickwinkel legen wir bei allen drei Eigenschaften auf die Bedingungen, unter denen diese Eigenschaften für die Spezies von Vorteil sind, da diese Situationen markieren, in denen sich diese Merkmale evolutionär durchsetzen können.

Wir werden zeigen, dass diese drei Eigenschaften entweder die Speziesabundanz oder die Speziesdiversität im Ökosystem erhöhen können. Reservoir-basierte Verteidigung der Beute kann sowohl die Beute- als auch die Räuberdichte erhöhen und ist stets dann von Vorteil für die Beute, wenn die Räuberdichte nicht zu klein und die Kosten für Verteidigung nicht zu hoch sind.

Stochastische Migration kann die lokale und regionale Diversität in einer Metagemeinschaft erhöhen; ersteres sogar im Limes sehr seltener Migrationsereignisse. Wir werden zeigen, dass sich die Diversitätssteigerung auf zwei Effekte zurückführen lässt, nämlich den sogenannten Rettungseffekt und dynamische Koexistenz. Dabei profitieren vor allem Spezies vom zweiten trophischen Level von diesen Effekten, während Spezies vom dritten trophischen Level nur von Migration profitieren können, wenn die Migrationsrate hoch ist.

Als letztes werden wir das enorme Ausmaß der Merkmalvariabilität in Pflanzen untersuchen. Wir werden zeigen, dass Variabilität in den Verteidigungs- und/oder Nährstoffkonzentrationen der Blätter *an sich* von Vorteil sein kann für die Pflanze und damit einen Grund darstellt, warum sich eine derart große Variabilität in diesen Merkmalen entwickelt haben könnte. Dabei werden wir zeigen, dass es ausschlaggebend sein kann das Präferenzverhalten der Herbivoren zu berücksichtigen. Im Speziellen werden wir zeigen, dass eine Pflanze von Verteidigungs- und Nährstoffvariabilität *an sich* profitiert, wenn sie hauptsächlich von Spezialisten befressen wird und diese für sich optimale Präferenz zeigen.

Am Ende dieser Thesis werden wir basierend auf diesen Ergebnissen diskutieren, wie diese drei Eigenschaften die Stabilität des Ökosystems beeinträchtigen können.

Abstract

Ecosystems undergo permanent changes. Due to human impact, several of these changes accelerate, like the climate change and the immigration rate of invasive species. Humanity is interested in the enduring stability of the ecosystem in which it lives and of which it is part of. Indeed, several features of species could be identified that can influence the stability of ecosystems. As these features can change due to an evolutionary adaptation to the current conditions, it is important to understand under which conditions a specific feature is beneficial for a species.

In this thesis, we investigate three features of species that can influence the stability of ecosystems, namely, prey defense against predator attacks, migration of species between habitats, and intraspecific trait variability in plants. More precisely, we consider reservoir-based defense, which means that the prey has a secretion reservoir that is biosynthetically refilled over time. The prey uses a certain amount of secretion to defend against a predator attack and is inedible as long as it stores at least this amount of secretion. Concerning the migration of species, we will focus on small migration rates for which stochastic effects become relevant, i.e. we analyze the so-called stochastic migration. Finally, we consider that plant individuals within one species or parts of one plant individual differ in their traits and we analyze the impact of this variability on herbivores. Especially, we focus for all three features on the conditions under which the features are beneficial for the species, as representing situations in which these features are evolutionary advantageous.

We will show that all three features enhance either species abundance or species diversity in the considered system. Reservoir-based defense can increase both the prey and predator density and is beneficial for the prey when the predator density is not too low and the costs for defense are not too high.

Stochastic migration can increase the local and regional diversity in metacommunities; the former even in the limit of very rare migration events. We show that this diversity increase can be ascribed to two effects, namely, the rescue effect and dynamical coexistence. Especially, species of the second trophic level benefit from these effects while species of the third trophic level only benefit from migration when migration rates are high.

Finally, we focus on the enormous extent of trait variability in plants. We show that variability in the defense and/or nutrient level of the leaves can *per se* be beneficial for the plant. We hence present a reason why this large trait variability may have evolved. Furthermore, we show the crucial impact of herbivore preference on these findings. Especially, we find that a plant can *per se* benefit from large nutrient and defense level variability when it is mainly attacked by specialists that have optimal preference.

At the end of this thesis, we discuss, based on these results, how these three features may affect the stability of ecosystems.

Contents

1 Introduction

The ecosystems[1] on earth are prone to environmental variation such as climate changes and fragmentation. The extent of these changes increases due to rising anthropogenic influence on the biosphere, i.e. the global ecosystem (Loreau and de Mazancourt, 2013; Hautier et al., 2015). Since humanity is one part of the ecosystems on earth and lives from its goods, the long-term sustainability of our ecosystems in view of these environmental changes is a central concern of humanity (Cardinale et al., 2012). Preserving our ecosystems is thus not just an idealistic goal, but is also important for economics (Perrings et al., 1992). Consequently, identifying and understanding mechanisms that enhance the stability of ecosystems has been a central topic in ecology for decades (May, 1972, 1973, 2001; McCann, 2000).

Due to the complexity of ecosystems it is difficult and sometimes impossible to empirically investigate whether factors enhance or decrease the stability of real-life ecosystems. Consequently, theoretical ecology represents an important part of these investigations. The complexity of ecosystem dynamics manifests for instance in chaotic behavior, that has been found in experiments (Becks et al., 2005; Benincà et al., 2008) and theoretical models (Hastings and Powell, 1991; Tanabe and Namba, 2005), and stochastic effects that can play an important role in ecosystems (Krkošek et al., 2011; Antonovics and Edwards, 2011; Higgins et al., 1997). Furthermore, ecosystems undergo bifurcations, which may lead to dramatic changes (so-called critical transitions (Scheffer, 2009)), such as extinction avalanches (Kuznetsov, 2013; Scheffer et al., 2009). As physicists (and mathematicians) know such complex dynamics from other parts of physics and have developed appropriate tools for investigating them, several theoretical ecologists are physicists or mathematicians by training.

Maybe because of these interdisciplinary working surroundings, multiple different measurements of (ecosystem) stability arose, which can be roughly categorized in (i) resilience (time until a system returns towards its equilibrium in turn of a perturbation), (ii) resistance (the degree to which a system changes in turn of a perturbation), and (iii) variability (the variance of species population over time) (Pimm, 1984).

Until today, researchers have identified several effects and mechanisms that enhance the stability in ecological systems in some measure. For instance, high availability of limiting resources can destabilize ecological systems (Rosenzweig, 1971; Vos et al., 2004b), also known as “paradox of enrichment” (Rosenzweig, 1971). Contrariwise, features that decrease the predation pressure (top-down control) in an ecosystem are attributed stabilizing effects, such as allometric scaling[2] (Yodzis and Innes, 1992; Brose et al., 2006b; Otto et al., 2007), weak interactions (McCann et al., 1998), predator interference (Rall et al., 2008), trait variability (Okuyama, 2008; Gibert and Brassil, 2014; Esquinas-Alcázar, 2005; Crutsinger et al., 2008), and various types of adaptive behavior (Valdovinos et al., 2010; Kondoh, 2006; Heckmann et al., 2012; Uchida et al., 2007; Fasham et al., 1990; Abrams, 2000). The latter includes adaptive foraging (Kondoh, 2006; Heckmann et al., 2012; Uchida et al., 2007), adaptive prey switching (Fasham et al., 1990; Valdovinos et al., 2010), prey defense against predator attacks (Vos et al., 2004a,b; Abrams and Walters, 1996; Ruxton and Lima, 1997; Bohannan and Lenski, 1999; Genkai-Kato and Yamamura, 1999), or adaptive prey behavior in response to predation risk (Abrams, 2000; Valdovinos et al., 2010). On global scale, migration or dispersal between habitats has been found to enhance the stability of ecological systems (Holyoak and Lawler, 1996; Hauzy et al., 2010; Plitzko and Drossel, 2014; Scheffer and De Boer, 1995; Gravel et al., 2016).

However, several of these stability-enhancing effects are not completely understood and in this thesis, we tackle open questions concerning three of them, namely

1. prey defense against predator attacks (Vos et al., 2004a,b; Abrams and Walters, 1996; Ruxton and Lima, 1997; Bohannan and Lenski, 1999; Genkai-Kato and Yamamura, 1999),
2. migration[3] of species between habitats (Holyoak and Lawler, 1996; Hauzy et al., 2010; Plitzko and Drossel, 2014; Scheffer and De Boer, 1995), and

[1] An ecosystem is “the complex of living organisms, their physical environment, and all their interrelationships in a particular unit of space” (Collins English Dictionary, 2019).

[2] See Section 2.3 for details.

[3] We will use the term migration to describe the steady biomass flow between habitats. Often, this term is used to describe periodic movements, for instance depending on the season as bird migration (Clobert et al., 2012). To comply with our paper (Thiel and Drossel, 2018), we do not use the term migration in this sense.

3. intraspecific trait variability, which means that populations, individuals, or parts of an individual differ in their traits (Agashe, 2009; Okuyama, 2008; Gibert and Brassil, 2014; Doebeli, 1997).

In our investigations, we do not focus exclusively on stability, but we want to broaden the general knowledge of these topics and understand the mechanisms underlying observed phenomena in nature. Especially, we will discuss under which conditions these features are advantageous for a species, since these may lead to increasing occurrence of this feature with proceeding time through natural selection[4] in real-life ecosystems. We thus provide reasons why and under which conditions these features may have evolved.

In order to distill the impact of each feature on the considered ecological system, we investigate them separately using a model that was constructed specially for this purpose. We thus present each of these studies in separate chapters including an introduction to the relevant knowledge of this topic as well as an explanation of the considered model. Nevertheless, all models are based on some general theory which is presented in Chapter 2.

In Chapter 3, we focus on prey defense against predator attacks which represents a certain type of adaptive behavior and is known to enhance the stability of an ecosystem (Vos et al., 2004a,b; Abrams and Walters, 1996; Ruxton and Lima, 1997; Bohannan and Lenski, 1999; Genkai-Kato and Yamamura, 1999). There are, however, several types of defense mechanisms and the stability enhancing effect of defense has not been shown for reducible defense which is widespread among invertebrates[5] (Eisner et al., 1961; Eisner, 2003; Berenbaum, 1995; Johnson et al., 2006b). In this thesis, we fill this gap. We focus on reservoir-based defense which is based on secretions that are stored in a reservoir. Upon attack, the prey releases a certain amount of these secretions to defend itself and is inedible as long as it stores at least this amount of secretion. After the attack, the secretions are biosynthetically restored over time. In particular, we investigate under which conditions reservoir-based defense is beneficial for the prey as defense includes costs.

In Chapter 4, we investigate the impact of migration on an ecosystem. Although several studies found that migration enhances the stability of ecosystems (Holyoak and Lawler, 1996; Hauzy et al., 2010; Plitzko and Drossel, 2014; Scheffer and De Boer, 1995), much less is known about the impact of migration on a complex food web when migration rates are small. In this case, stochastic effects become important and a deterministic modeling is inappropriate. Stochastic migration is thus topic of one part of this thesis. In particular, we are interested in the mechanisms that drive the observed phenomena and in the characteristics of species that mainly benefit from stochastic migration.

In Chapter 5, we focus on intraspecific trait variability, which means that traits differ among populations, individuals, or even within individuals of one species (Herrera, 2009; Gibert and Brassil, 2014; Bolnick et al., 2011). In predator-prey systems, intraspecific trait variability can enhance the stability of an ecosystem (Okuyama, 2008; Gibert and Brassil, 2014). In this thesis, we, however, focus on the enormous trait variability in plant species and its impact on the ecosystem, especially on insect-herbivores. For this plant-herbivore system, the predator-prey model used in (Okuyama, 2008; Gibert and Brassil, 2014) is inappropriate (s. Section 5.2 for details). Despite of several empirical studies concerning the impact of intraspecific trait variability in plant species on the ecosystem (Jung et al., 2010; Whitlock et al., 2007; Kotowska et al., 2010; Crutsinger et al., 2006), there is still a knowledge gap about why plants show such a large intraspecific trait variability. In this thesis, we focus on the *per se* impact of intraspecific trait variability on the plant population. Intraspecific trait variability can lead to different mean herbivore responses compared to considering just the mean trait value due to non-linear averaging (Bolnick et al., 2011; Wetzel et al., 2016; Ruel and Ayres, 1999). When trait variability decreases the mean herbivore response, it is *per se* beneficial for the plant and may thus be an evolutionary advantage. Consequently, intraspecific trait variability may be a piece of the puzzle to explain the large intraspecific trait variability found in plants (Herrera, 2009; Siefert et al., 2015). In particular, we investigate the impact of herbivore preference, different herbivore specialization strategies, and a correlation between the nutrient and the defense level of a leaf on our findings.

Finally, in Chapter 6, we summarize and discuss the results of the proceeding three sections.

[4] Natural selection is "a process resulting in the survival of those individuals from a population of animals or plants that are best adapted to the prevailing environmental conditions. The survivors tend to produce more offspring than those less well adapted, so that the characteristics of the population change over time, thus accounting for the process of evolution" (Encyclopaedia Britannica inc., 2019).

[5] Animal species that have no backbone.

2 Basics

In this thesis, we tackle open questions concerning three features of species – reducible defense, (stochastic) migration, and intraspecific trait variability – in antagonistic systems. We use population dynamics in order to describe and model these systems, whereby the exact equations used will differ between the projects due to the varying requests. The simplest antagonistic system is a consumer-resource interaction which shall be described in the following and will serve as a basis for all three projects. Note, that we use this term such that consumer-resource interactions include predator-prey, plant-herbivore, and host-parasite interactions (Getz, 2011).

2.1 Population dynamics in a consumer-resource system

First, we must think about the definition of a species. In this thesis, we examine trophic species, which means that species with the same consumers and resource species are combined in one functional group (Bornholdt and Schuster, 2006; Williams and Martinez, 2000). Hence, a species in the biological meaning may belong to different trophic species during its lifetime (Bornholdt and Schuster, 2006).

We describe the dynamics in the consumer-resource system on population basis. A population is defined as a group of individuals from one species living in a delimited area, that represents a potential reproductive community (Smith and Smith, 2009). We use the bioenergetics approach developed by Yodzis and Innes (1992) to describe population dynamics for a consumer density C and a resource density R, i.e. the number of individuals per area,

$$\begin{aligned} \frac{\mathrm{d}R}{\mathrm{d}t} &= rR\left(1-\frac{R}{K_R}\right) - F(R)C - \alpha_R R \\ \frac{\mathrm{d}C}{\mathrm{d}t} &= \lambda F(R)C - \alpha_C C - \beta_C C^2 . \end{aligned} \tag{2.1}$$

The first term represents logistic growth of the resource with the growth rate r and the carrying capacity K_R denoting the largest number of resource individuals per area that can coexist. The functional response $F(R)$ describes the consumption rate per consumer and is explained in detail in Section 2.2. The assimilation efficiency of the consumer λ denotes the number of resource individuals that have to be consumed to obtain enough food for producing one consumer individual. Metabolic loss of consumer and resource is included in the second and third term of the corresponding equation with respiration rates α_C and α_R, respectively. Finally, we consider quadratic loss due to intraspecific competition of consumers for other resources than food with a competition rate β_C, for instance for nesting sites. Additionally, this term can model disease spreading.

Note, that this approach does not need to be appropriate for all consumer-resource systems observed in nature.

2.2 Functional response

The functional response, i.e. the consumption rate per consumer, can be crucial for the dynamical behaviour of the system. A simple choice is a linear function,

$$F(R) = aR , \tag{2.2}$$

with the attack rate a, which describes the area scanned per consumer and time interval. This functional response is known as Holling Type I functional response and has some unrealistic features as for instance that the capture rate per consumer is unlimited when the resource density increases (cp. Fig. 2.1). Holling (1965) suggested the so-called Holling Type II functional response which is based on the idea that the consumer has a delimited time. This time is dividable in time for searching for food T_S and in time for handling it T_h, i.e. for consuming and digesting the food. With the further assumption of random encounters between consumer and resource species, one obtains the Holling Type II functional response

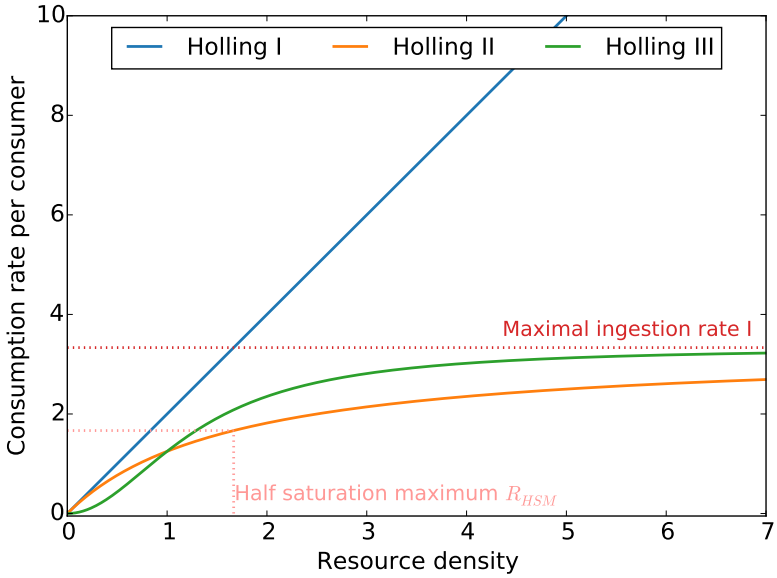

Figure 2.1.: Holling Type I, II, and III functional response as a function of the resource density. We marked the maximal ingestion rate I and the half saturation maximum R_{HSM} for the Holling Type II functional response as dotted lines. We used an attack rate $a = 2$ and a handling time $T_h = 0.3$ for this plot.

$$F(R) = \frac{aR}{1 + aT_hR}, \tag{2.3}$$

that is a linear function in the limit of small resource densities R and saturates for large resource densities R (cp. Fig. 2.1). The derivation of the Holling Type II functional response is shown in detail in Appendix A. The maximal ingestion rate is defined by the handling time T_h via

$$I = \lim_{R\to\infty} F(R) = \lim_{R\to\infty} \frac{aR}{1 + aT_hR} = \frac{1}{T_h}, \tag{2.4}$$

and the half saturation maximum (HSM) is at

$$\begin{aligned} \frac{1}{2T_h} &= \frac{aR_{\text{HSM}}}{1 + aT_hR_{\text{HSM}}} \\ \frac{1}{2T_h} &= \frac{1}{2}aR_{\text{HSM}} \\ \Rightarrow R_{\text{HSM}} &= \frac{1}{aT_h}, \end{aligned} \tag{2.5}$$

as illustrated in Fig. 2.1. The half saturation maximum thus describes the resource density for which the consumer can feed with half of its consumption rate maximum.

The Holling Type II functional response is well-established and often used in theoretical ecology (Plitzko and Drossel, 2014; Binzer et al., 2012; Hamm and Drossel, 2017) due to its simplicity and the ecologically convincing assumptions used for its derivation. For these reasons, we will also use the Holling Type II functional response in this thesis. For the sake of completeness, we nevertheless want to mention that there are many more functional responses often used in theoretical ecology like the s-shaped Holling Type III functional response (Holling, 1965), where the resource density appears in a higher dimension than one what leads to a smaller slope when resource density is low (s. Fig. 2.1). This models intelligent consumers that avoid spending too much energy on hunting rare resource species (Pascual et al., 2006). Some studies found that a Holling Type III functional response leads to more stable food webs (Valdovinos et al., 2010; Williams and Martinez, 2004b), however, attended by a loss of a convincing derivation. Another often used version is the Beddington functional response (Beddington, 1975), which additionally considers the wasted time when two consumers meet and thus includes intraspecific competition of consumers for food.

2.3 Allometric scaling

Empirical studies found that consumers are typically larger than their resource species (about 0.5-4 orders of magnitude) (Brose et al., 2006a). In particular, this is true for predator-prey interactions (Brose et al., 2006a). The time scales on which the metabolism of species happens depend on their body mass and thus their size (Brown et al., 2004); species with a higher body mass typically have a slower metabolism. This influences the biological rates considered in our equations, such as the growth and respiration rate (Brose et al., 2006a). More precisely, it is found that the size-related rates can be expressed in terms of power functions of the form

$$X_i = X_0 m_i^b \,, \tag{2.6}$$

with a normalization constant X_0, the body mass m_i of the species i, and the allometric exponent b (Brown et al., 2004). Based on metabolic theory (Brown et al., 2004), the allometric exponents of several biological rates have been predicted:

- The respiration rate of species i: $\alpha_i = \alpha_0 m_i^{-0.25}$ (Brown et al., 2004; Heckmann et al., 2012).
- The maximal ingestion rate of consumer i: $I_i = I_0 m_i^{0.75}$. Hence, following Eq.(2.4) and taking into account that the time needed to handling a resource individual should be proportional to its body mass, the handling time scales as $T_{h,ij} = T_{h,0} m_i^{-0.75} m_j$ (Heckmann et al., 2012).
- The attack rate of consumer i concerning resource j: $a_{ij} = a_0 m_i^{0.75}$. This is based on the finding that the half saturation biomass density is independent of body mass (Heckmann et al., 2012; Yodzis and Innes, 1992; Brose et al., 2006b). This means $B_{\mathrm{HSM},j} = R_{\mathrm{HSM},j} m_j = \frac{m_j}{a_{ij} T_{h,ij}}$ (s. Eq.(2.5)), as the biomass density describes the accumulated body mass over all individuals of a species j per area.
- The competition rate of consumer i: $\beta_i = \beta_0 m_i^{0.75}$. This is based on the findings that the equilibrium population densities B_i^{eq} scale like $B_i^{\mathrm{eq}} = B_0^{\mathrm{eq}} m_i^{-0.75}$ (Heckmann et al., 2012; Brown et al., 2004) and that the inverse of the competition rate limits population growth comparable to the carrying capacity (Thiel et al., 2018).

Indeed, several empirical studies found similar exponents (Rall et al., 2012; Binzer et al., 2012). One explanation for the recurrent $\frac{1}{4}$ powers may be the fractal-like structure of the surface and the volume (and thus the mass) of the considered bodies (Brown et al., 2004). Since exchanges (e.g. heat) of the body volume with the environment typically takes place via the body surface one may infer that the respiration rate of a whole organism scales with $m_i^{2/3}$. However, taking into account that for instance the branching networks of respiratory and circulatory systems considerably increase the surface yields a scaling law of the respiration rate of a whole organism of $m_i^{3/4}$ (Brown et al., 2004; Savage et al., 2004).

Furthermore, theoretical studies showed that allometric scaling enhances the stability of ecological systems (Heckmann et al., 2012; Brose et al., 2006b). Hence, allometric scaling may represent one important feature to explain the stability of complex food webs. We will thus use these scaling laws in order to find realistic values for the biological rates in our models.

2.4 Extensions

In the following, we expand this simple and well-analyzed consumer-resource model (s. Eq.(2.1)) by different aspects which have in common to be mechanisms that may affect the stability of ecological systems.

First, we include reservoir-based defense. This means that the prey has a reservoir for storing secretion and can defend itself by releasing part of these secretions. After the attack, the secretions are biosynthetically restored over time. Hence, we expand the consumer-resource model (s. Eq.(2.1)) via introducing an equation to model secretion and to determine the defended prey. Additionally, we need to adjust the functional response (s. Eq.(2.3)) in order to take into account that defended prey is inedible.

In the second part, we investigate the effect of stochastic migration on metacommunities, that are complex food webs consisting of several species which are located on a spatial web (Holyoak et al., 2005). So, we consider that migration events between habitats are rare, for instance because they are far apart from each other, such that it

is necessary to model migration as a stochastic process. Hence, we need to expand the consumer-resource model (s. Eq.(2.1)) to multiple species on several patches. Additionally, we need to introduce an equation to model migration (as a stochastic process).

In the last part, we focus on a plant-insect herbivore system where the plant leaves differ in their nutrient and/or their defense level. For this investigation, we use a generation-based approach in order to take the typical time scales on which the trait distribution changes into account compared to the lifetime of the insect herbivores. In this generation-based model, we include that plant leaves differ in their traits and that herbivores can show preference for leaves with certain traits. In principle, the generation-based approach can be derived from the consumer-resource model (s. Eq.(2.1)) (s. Appendix E).

3 Reducible defense

In this chapter, we will investigate the impact of incorporating prey defense in a predator-prey system (cp. Eq.(2.1)).

Defense mechanisms are widespread among animal species (and plant species; s. Section 5.5) and have the potential to considerably change the dynamics and stability of ecological systems (Vos et al., 2004b,a; Abrams and Walters, 1996). There are three major categories of defense mechanisms:

1. Permanent, constitutive defenses;
2. Temporary, inducible defenses;
3. Permanent reducible defenses.

Permanent, constitutive defenses are always present in the species and include carapaces, horns, trichomes[1], and crypsis[2] (Mauricio and Rausher, 1997; Lankau, 2007). This type of defense leads to altered interaction parameters, for instance increased handling times or reduced attack rates (Abrams and Walters, 1996; Bohannan and Lenski, 1999) (cp. Section 2.2), but also includes permanent energetic costs for maintaining the defense mechanism. When attacks are rare or happen in episodes these costs might exceed the benefits of this defense mechanism (Gaschler, 2019), such that many species have evolved temporary defense mechanisms that are activated after a non-lethal predator attack. These are called temporary, inducible defenses and include changes in behavior, morphology[3], and life history (Hammill et al., 2010). Permanent reducible defenses are regularly found among terrestrial and marine animals, especially among invertebrates[4] (Heethoff and Rall, 2015; Eisner et al., 1961; Eisner, 2003; Johnson et al., 2006b). This type of defense, also known as reservoir-based defense (Brückner and Heethoff, 2018), is based on secretions that are stored in a reservoir. Upon attack, the prey releases part of these secretions to defend itself. After the attack, the secretions are biosynthetically restored over time.

Many empirical studies document defense mechanisms in a large variability of different species (Heethoff et al., 2011; Bohannan and Lenski, 1999; Huffaker et al., 1963; Karban and Baldwin, 2007), however, there are only few theoretical models and studies that investigated the impact of defense mechanisms on ecosystems. These studies have shown that constitutive and inducible defense mechanisms of prey against consumption can enhance the stability and species abundance in an ecosystem (Vos et al., 2004a,b; Abrams and Walters, 1996; Ruxton and Lima, 1997; Bohannan and Lenski, 1999; Genkai-Kato and Yamamura, 1999), but little is known about reducible, reservoir-based defense. Especially, the impact of reservoir-based defense on the long time dynamics of a predator-prey system was unknown. In our paper "The effect of reservoir-based chemical defense on predator-prey dynamics", which was created in collaboration with Andreas Brechtel, Adrian Brückner, Michael Heethoff, and Barbara Drossel, we filled this gap. We investigated reducible defense in a predator-prey model and we could show that reducible defense can increase population densities of both predator and prey (Thiel et al., 2018). In this chapter, we will present these results in detail, but first we need to introduce the model incorporating reducible defense that is based on the consumer-resource population dynamics shown in Eq.(2.1).

This work was published in "Theoretical Ecology" (Thiel et al., 2018). Adrian Brückner and Michael Heethoff provided general advice concerning biological questions and were leading for the identification of the problems we investigated in this study. Our model is inspired by the work of Heethoff and Rall (2015) and Andreas Brechtel and Barbara Drossel supported its construction with helpful discussions. Furthermore, Andreas Brechtel deduced the formula to describe the fraction of defended prey and performed stochastic simulations to validate the expression (s. Appendix B). Barbara Drossel helped condense different models used to answer different questions to a single set of equations which is presented here. Everything else, i.e. the construction (except for the formula to describe the fraction of defended prey) and implementation of the model, the simulations, the interpretation of the results, and the draft of the paper manuscript were done by the author of this thesis. Concerning the latter, Barbara Drossel, Adrian Brückner, and Michael Heethoff also provided linguistic revision.

[1] These are small hair-like structures that can in principle fulfill different functions in an organisms (Mauricio and Rausher, 1997). Defense is one example.

[2] A species adapts its appearance to avoid detection by predators (Begon et al., 1997).

[3] This means the structure or form of the species (Begon et al., 1997).

[4] Animal species that have no backbone.

3.1 The model

In this section, we introduce our model to investigate the impact of reservoir-based defense. Hence, we expand the consumer-resource model (s. Eq.(2.1)) via introducing an equation to model secretion S and to determine the fraction of defended prey. Additionally, we deduce a functional response $F(B,S)$ (cp. Eq.(2.3)) that takes into account that defended prey is inedible. Hence, we describe the population dynamics of the prey density B and the predator density P via

$$\begin{aligned} \frac{\mathrm{d}B}{\mathrm{d}t} &= rB\left(1-\frac{B}{K_B}\right) - F(B,S)P - \alpha_P P \\ \frac{\mathrm{d}P}{\mathrm{d}t} &= \lambda F(B,S)P - \alpha_P P - \beta_P P^2 \,. \end{aligned} \tag{3.1}$$

3.1.1 Including defense in the functional response

In order to find an appropriate expression for the functional response that includes reducible defense, we use a similar approach as used by Holling for deriving his Type II functional response (Holling, 1959a,b) (s. Appendix A for comparison). We consider a fixed time interval T. The predator can use this time for

- the search for food,
- the consumption and the handling of undefended prey, and
- unsuccessful attacks on defended prey, since the predator needs time to clean his mouth parts from secretion (Heethoff et al., 2011).

In terms of an equation, this means

$$T = T_s + T_h Y + T_w Z \,, \tag{3.2}$$

with the handling time T_h per undefended prey individual, the number of undefended prey individuals Y consumed per predator in time T, the time wasted on unsuccessful attacks T_w per defended prey individual, and the number of defended prey individuals Z being attacked per predator in time T. The number of undefended prey individuals consumed per predator, Y, depends on the time that the predator can use for searching, T_s, and the discovery rate a that describes the area scanned per predator and time interval,

$$Y = aT_s(1-D(S))B \,. \tag{3.3}$$

Here, B is the prey density and $D(S)$ denotes the fraction of defended prey, such that the density of undefended prey individuals is $(1-D(S))B$. Consequently, we find for the number of defended prey individuals being attacked per predator Z

$$Z = aT_s D(S)B \,. \tag{3.4}$$

Including Eq.(3.3) and (3.4) in Eq.(3.2) yields

$$T = T_s\left(1 + aT_h(1-D(S))B + aT_w D(S)B\right) , \tag{3.5}$$

and the time available for searching can be expressed as

$$T_s = \frac{T}{1 + aT_w D(S)B + aT_h\left(1-D(S)\right)B} \,. \tag{3.6}$$

We obtain the functional response, i.e. the number of undefended prey individuals consumed per predator and per time interval T, by including Eq.(3.6) in Eq.(3.3)

$$F(B,S) = \frac{Y}{T} = \frac{a\,(1-D(S))\,B}{1 + aT_w D(S)B + aT_h\,(1-D(S))\,B}\,. \tag{3.7}$$

By comparing this result with the regular Holling Type II functional response introduced in Section 2.2, the reader will see that the functional response defined in Eq.(3.7) has an additional term in the denominator describing the time loss due to unsuccessful attacks on defended prey. Consequently, when all prey is undefended (i.e. $D(S) = 0$) or the predator wastes no time on unsuccessful attacks (i.e. $T_w = 0$) the functional response defined in Eq.(3.7) corresponds to the regular Holling Type II functional response (cp. Eq.(2.3)).

The maximal ingestion rate is

$$I = \lim_{B\to\infty} F(B,S) = \frac{1-D(S)}{T_w D(S) + T_h\,(1-D(S))}\,. \tag{3.8}$$

It depends on the fraction of defended prey $D(S)$ as well as the time wasted on unsuccessful attacks T_w and is thus smaller than the maximal ingestion rate of the regular Holling Type II functional response when $D(S), T_w > 0$ (cp. Eq.(2.4)). Similarly, the half saturation maximum, i.e. the prey density for which the predator can consume with half of its maximal ingestion rate, is

$$B_{\mathrm{HSM}} = \frac{1}{aT_w D(S) + aT_h(1-D(S))} = \frac{1}{aT_h + a(T_w - T_h)D(S)}\,, \tag{3.9}$$

and is thus larger than those of the regular Holling Type II functional response when $T_h > T_w$ and smaller in the opposite case due to the considerable lower maximal ingestion rate I (cp. Eq.(2.5)).

3.1.2 Equation for secretion

In order to model the fraction of defended prey and prey defense itself with time, we use the average amount of secretion per prey individual S as model variable. Prey regenerates secretion with a rate p_S and excretes a fixed amount of secretion to defend itself against a predator attack, which we call transferring constant e_S. Hence, we describe secretion dynamics via

$$\frac{\mathrm{d}S}{\mathrm{d}t} = p_S\left(1 - \frac{S}{K_S}\right) - e_S F_d(B,S)\frac{P}{B}\,, \tag{3.10}$$

where K_S is the reservoir size and thus the maximum amount of secretion that can be stored by one prey individual. The function $F_d(B,S)$ represents the disarming rate per predator and can be derived analogously to the functional response by including Eq.(3.6) in Eq.(3.4), leading to

$$F_d(B,S) = \frac{aD(S)B}{1 + T_w aD(S)B + T_h a\,(1-D(S))\,B}\,. \tag{3.11}$$

Consequently, predator individuals can help each other to disarm prey and thus benefit from an abundant population. This effect is called apparent facilitation (Heethoff and Rall, 2015) and is a special characteristic of reducible defense compared to the other defense mechanisms.

3.1.3 Fraction of defended prey

We still need an appropriate expression to describe the fraction of defended prey $D(S)$ as a function of the average amount of secretion S per prey. For finding this expression, we focus on the limiting case, i.e. the smallest amount

of secretion required to be defended. This is the amount of secretion that is excreted per predator attack, which is the transferring constant e_S. Hence, the amount of secretion stored by undefended prey is distributed in the interval $[0, e_S)$, and the secretion of defended prey is distributed in the interval $[e_S, K_S]$, with $e_S \leq K_S$. As no further information is known about the distribution of secretion among the prey individuals we use a uniform distribution and calculate the weighted mean,

$$S = \frac{e_S}{2}(1 - D(S)) + \frac{K_S + e_S}{2} D(S) = \frac{e_S + K_S D(S)}{2} . \tag{3.12}$$

The fraction of defended prey is thus

$$D(S) = \begin{cases} 0 & S \leq \frac{e_S}{2} , \\ \frac{2S - e_S}{K_S} & \text{if} \quad \frac{e_S}{2} < S < \frac{K_S + e_S}{2} , \\ 1 & S \geq \frac{K_S + e_S}{2} . \end{cases} \tag{3.13}$$

In order to value the quality of this approximation, we additionally performed individual-based stochastic simulations where we explicitly consider the amount of secretion stored by each prey individual, which changes due to encounters with predators and refilling dynamics. The details of these stochastic simulations are explained in Appendix B, where we also show the fraction of defended prey $D(S)$ as a function of the mean defense level S that results from these simulations. We find that the simple function (3.13) leads to qualitative correct results and is even quantitatively appropriate when e_S is of the order of magnitude used in most simulations in this thesis. We thus use the mean-field expression in Eq.(3.13) for the rest of this chapter.

3.1.4 Metabolic loss

The survival of species is determined by optimal investment strategies of available energy. For instance, there is a trade-off between investing in growth/ reproduction and defense such that the amount of energy provided for defense is limited (Bryant et al., 1983; Dicke, 2000; Valdovinos et al., 2010; Matsuda et al., 1996). We thus explicitly introduce metabolic costs for defense in the metabolic loss term.

We assume that the metabolic costs for defense arise due to maintaining the reservoir and due to producing secretion. Hence, we define the prey respiration rate α_B as

$$\alpha_B = \vartheta K_S + \eta p_S + \kappa . \tag{3.14}$$

The first term describes the metabolic cost for maintaining a reservoir with the capacity K_S, which arises due to installing and maintaining the structures of the reservoir (Purrington, 2000). The second term represents the cost for producing secretion, which we assume to be proportional to the regeneration rate p_S. This is a simplifying assumption that is appropriate if the cost for *maintaining the mechanisms* for fast refilling exceeds those of the *refilling process*. Besides, this assumption is appropriate if p_S is evolved such that it correlates with the actual depletion rate. The third term includes the metabolic losses due to processes unrelated to defense. As the parameters η and ϑ determine the costs for defense they represent important parameters of the model.

Since the metabolic loss effectively limits the growth of prey via

$$\begin{aligned} \frac{\mathrm{d}B}{\mathrm{d}t} &= rB\left(1 - \frac{B}{K_B}\right) - F(B,S)P - \alpha_B B \\ &= \underbrace{(r - \alpha_B)}_{r_{\text{eff}}} B - r\frac{B}{K_B} - F(B,S)P , \end{aligned} \tag{3.15}$$

we can display the trade-off between defense and growth. The effective growth rate of prey is given by

$$r_{\text{eff}}(p_S, K_S) = r - \kappa - \eta p_S - \vartheta K_S . \tag{3.16}$$

3.1.5 The model in a nutshell

In a nutshell, population dynamics in our predator-prey model are described by the following equations

$$\begin{aligned}\frac{\mathrm{d}B}{\mathrm{d}t} &= r_{\text{eff}}B - \frac{r}{K_B}B^2 - F(B,S)P\,,\\ \frac{\mathrm{d}S}{\mathrm{d}t} &= p_S\left(1-\frac{S}{K_S}\right) - e_S F_d(B,S)\frac{P}{B}\,,\\ \frac{\mathrm{d}P}{\mathrm{d}t} &= \lambda F(B,S)P - \alpha_P P - \beta_P P^2\,,\end{aligned} \tag{3.17}$$

with the consumption rate per predator $F(B,S)$ (s. Eq.(3.7)), the disarming rate per predator $F_d(B,S)$ (s. Eq.(3.11)), and the effective growth rate of prey r_{eff} (s. Eq.(3.16)).

3.2 Linear stability analysis

The long time dynamics of this system can be calculated analytically by identifying stable fixed points. With our choice of parameter values (s. Section 3.3 for details), no limit cycles are possible. In order to find the stable fixed points, we write Eq.(3.17) in the following form

$$\frac{\mathrm{d}\vec{x}}{\mathrm{d}t} = A\vec{x}\,, \tag{3.18}$$

with $\vec{x} = (B,S,P)$. The stability of the fixed points of the system (i.e. $(B,S,P) : \frac{\mathrm{d}B}{\mathrm{d}t} = \frac{\mathrm{d}S}{\mathrm{d}t} = \frac{\mathrm{d}P}{\mathrm{d}t} = 0$) can be determined by calculating the eigenvalues of the Jacobian of the matrix A at the considered fixed point. If the eigenvalues have a negative real part, the considered fixed point is stable which means that after a sufficiently long time and an appropriate choice of the initial conditions, the system will evolve towards this fixed point.

3.3 Choice of parameter values

In order to choose the parameter values, we used the oribatid mites (*Archegozetes longisetosus*) – rove beetle (*Stenus juno*) predator-prey system as our model system. This means that we either used measured values or, when we could not find an appropriate study, we calculated the parameter values via the measured masses of both species. These calculations are based on allometric scaling (cp. Section 2.3) and a temperature correction, which takes into account that biological rates are typically slower in colder environments (Binzer et al., 2012). Indeed, Binzer et al. (2012) found similar allometric exponents as introduced in Section 2.3. All parameter values are summarized in Tab. 3.1.

The values of the parameters that model defense are listed in Tab. 3.1(a) and are based on measurements in empirical studies – we choose similar values as in (Heethoff and Rall, 2015) for the reservoir size K_S, the wasted time T_w, and the regeneration rate of secretion p_S. Indeed, a similar value for the regeneration rate per dry weight is found for cockroaches (Farine et al., 2000; Baldwin et al., 1990) assuming a dry weight of 300 mg for the cockroach (Gilbert, 2011). Raspotnig (2006) found that the oribatid mite *Collohmannia gigantea* can defend against up to five attacks and Heethoff (2012) found similar values for the oribatid mite *A. longisetosus*. Based on these studies, we chose the transferring constant e_S, i.e. the amount of secretion that is released to defend against one attack.

The parameter values concerning predator-prey dynamics are listed in Tab. 3.1(b). For the assimilation efficiency, we use the value found in (Yodzis and Innes, 1992) for predators. The remaining parameters in Tab. 3.1(b) were calculated by using the scaling laws found in (Binzer et al., 2012) and assuming the same temperature and mass of prey and predator as in (Heethoff and Rall, 2015), which are listed in Tab. 3.1(c).

As the time wasted on unsuccessful attacks T_w is much smaller than the handling time T_h, a larger prey density is needed such that the predator can feed with half of its maximal ingestion rate compared to a system where prey is not able to defend against predator attacks (i.e. a regular Holling type II functional response; s. Eq.(3.9)).

We use two values for the carrying capacity of the prey K_B since the typical prey densities that are considered in experiments on short time scales (Heethoff and Rall, 2015; Heethoff et al., 2011; Brückner et al., 2016) are much

Table 3.1.: Parameter values used for modeling defense (Tab. 3.1(a)), predator-prey dynamics (Tab. 3.1(b)), and initial conditions (Tab. 3.1(c)).

(a) Secretion parameter based on (Heethoff and Rall, 2015; Baldwin et al., 1990; Farine et al., 2000).

Regeneration rate	Reservoir size	Transferring constant	Wasted time
p_S	K_S	e_S	T_w
$2\,\frac{\mathrm{ng}}{\mathrm{h}}$	100 ng	20 ng	0.5 s

(b) Parameter of predator-prey dynamics based on (Binzer et al., 2012; Yodzis and Innes, 1992).

Discovery rate	Assimilation efficiency	Handling time	Growth rate	Carrying capacity	Respiration rate of prey	Respiration rate of pred.	Competition rate
a	λ	T_h	r	K_B	α_B	α_P	β_P
$3\,\frac{\mathrm{cm}^2}{\mathrm{h}}$	0.85	0.6 h	$0.2\,\frac{1}{\mathrm{h}}$	$0.04\,\frac{1}{\mathrm{cm}^2}$/ $0.5\,\frac{1}{\mathrm{cm}^2}$	$5\cdot10^{-3}\,\frac{1}{\mathrm{h}}$	$2\cdot10^{-4}\,\frac{1}{\mathrm{h}}$	$0.2\,\frac{\mathrm{cm}^2}{\mathrm{h}}$

(c) Assumed masses and temperature based on (Heethoff and Rall, 2015) to calculate parameters of predator-prey dynamics (Tab. 3.1(b)), initial densities of predator P and prey B, and cost factors concerning regeneration and storing of secretion.

Mass of prey	Mass of predator	Temperature	Initial prey density	Initial predator density	Cost factor conc. K_s	Cost factor conc. p_S
m_B	m_P	T	B_{ini}	P_{ini}	ϑ	η
0.1 mg	3.5 mg	23 °C	$0.5\,\frac{1}{\mathrm{cm}^2}$	$0.05\,\frac{1}{\mathrm{cm}^2}$	$1\cdot10^{-5}\,\frac{1}{\mathrm{ng\,h}}$	$6\cdot10^{-4}\,\frac{1}{\mathrm{ng}}$

larger than those found in nature. In the first part of our investigation, we analyze the dynamics on short time scales and we thus use the larger value for the carrying capacity. We assume in this part that the prey has not been attacked for a significant time before our investigation starts such that their reservoirs are completely filled (i.e. $S_{\mathrm{ini}} = K_S$) and the prey and predator densities correspond to their carrying capacities, respectively (i.e. $B_{\mathrm{ini}} = K_B$; s. Tab. 3.1(c)). This corresponds to the conditions in the typical experiments, we used for comparison (Heethoff and Rall, 2015; Heethoff et al., 2011; Brückner et al., 2016). We hence use the initial prey densities considered in these experiments (s. Tab. 3.1(c)) to describe the carrying capacity for prey in this part. However, when we focus on the long time dynamics, we use the smaller value which is calculated according to (Binzer et al., 2012) and is thus of the typical order of magnitude found in nature.

In order to find a value for the competition rate, we assume that the growth rate divided by the carrying capacity of the predator is an appropriate choice since we could not find a study that quantifies this power law (i.e. β_0 in Section 2.3). This is based on the following idea: Competition is a limiting term of predator density that goes with P^2. Similarly, the growth rate r divided by the carrying capacity K_B limits the prey density in a quadratic manner, such that these limiting factors are comparable (cp. Eq.(3.17)). We calculated the growth rate and the carrying capacity according to (Binzer et al., 2012) with the mass of the predator and temperature as listed in Tab. 3.1(c).

The parameters that model the metabolic loss concerning the reservoir size K_S, ϑ, and the regeneration rate p_S, η, are listed in Tab. 3.1(c). For their derivation, we assume that $\kappa = 0.5\alpha$ and that the costs for maintaining the reservoir and for producing secretion are equal considering the empirically motivated values for the reservoir size K_S and the regeneration rate p_S in Tab. 3.1(a). This means

$$\vartheta K_S = \eta p_S = 0.25\alpha_B\,. \tag{3.19}$$

3.4 Research questions

We divide our investigation into two parts: First, we focus on the impact of reducible defense on the time scale of predator-prey interactions and neglect the much slower dynamics of reproduction. This scenario will act as

a point of comparison for typical experiments concerning the defense mechanism of oribatid mites (*Archegozetes longisetosus*) against a typical predator, namely the rove beetle (*Stenus juno*) (Brückner et al., 2016; Heethoff et al., 2011; Heethoff and Rall, 2015). In these experiments, the mites are captured in an arena after a long recovery time such that reservoirs are completely filled. After introducing the predator, the mites are observed for a certain time span (Heethoff et al., 2011). For this investigation on short time scales, we want to discuss:

- Whether our model behaves as expected and as observed in experiments under variation of the parameters modeling defense.
- Which is the best defense strategy to maximize lifetime during such a period of frequent attacks – having a large, initially completely filled reservoir or being able to fast refill the reservoir?
- Under which conditions is it beneficial to have no defense mechanism?

In the second part, we focus on the long time behavior of the model in order to compare it to the regular predator-prey model (cp. Eq.(2.1)). Here, we are interested in the following questions:

- Under which conditions is it beneficial for the prey to invest in defense, keeping in mind that this reduces the effective growth rate of the prey (cp. Eq.(3.16))?
- Can reducible defense enhance species abundance as observed for inducible and constitutive defense (Abrams and Walters, 1996; Vos et al., 2004a,b)?
- Under which conditions is coexistence of predator and prey possible?

In the following, we present our results concerning these research questions of the short and long time scale investigation.

3.5 Investigation on short time scales

In a first step, we focus on the time scale of predator-prey interactions and neglect the much slower dynamics of reproduction. We can thus distill the effect of prey defense on the predator-prey dynamics. This mirrors experimental studies (Heethoff and Rall, 2015; Brückner et al., 2016; Heethoff et al., 2011), where prey species have no chance to hide and thus to escape the predator. Hence, the time scales considered in these type of studies are shorter than the generation time of predator and prey.

Under this assumption, Eq.(3.17) describing population dynamics of a predator-prey system, where prey has evolved reservoir-based defense, changes to

$$\begin{aligned}\frac{\mathrm{d}B}{\mathrm{d}t} &= -F(B,S)P - (\kappa + \eta p_S + \vartheta K_S)B\,,\\ \frac{\mathrm{d}S}{\mathrm{d}t} &= p_S\left(1-\frac{S}{K_S}\right) - e_S F_d(B,S)\frac{P}{B}\,,\\ \frac{\mathrm{d}P}{\mathrm{d}t} &= 0\,.\end{aligned} \tag{3.20}$$

Hence, the predator density stays at its initial density during this investigation as it cannot reproduce. As in the empirical studies, we used for comparison (Heethoff and Rall, 2015; Brückner et al., 2016; Heethoff et al., 2011), we assume that the reservoirs are initially completely filled, i.e. $S(t=0) = S_{\mathrm{ini}} = K_S$, and the initial predator and prey densities listed in Tab. 3.1(c).

3.5.1 Impact of defense on feeding rates

In order to test our model, we first analyze whether the impact of prey defense on the dynamics of prey consumption meets our expectations. These are:

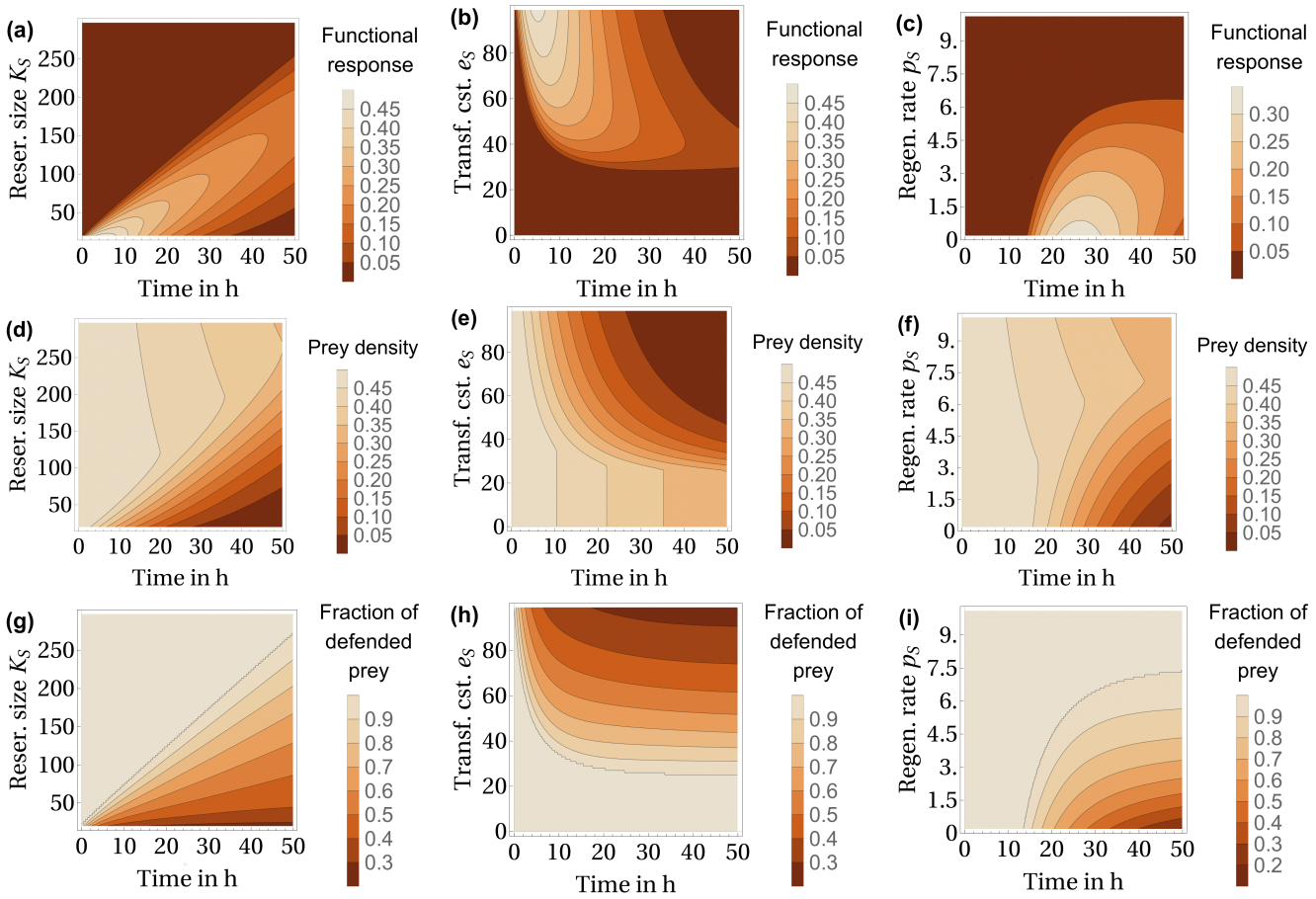

Figure 3.1.: The dynamics of prey consumption as a function of time and the three defense parameters K_S ((a), (d), (g)), e_S ((b), (e), (h)), and p_S ((c), (f), (i)). The different color shades indicate prey consumption rate ((a)-(c)), prey density ((d)-(f)), and the fraction of defended prey ((g)-(i)). The parameters that are not varied in a plot are set to the values given in Tab. 3.1.

- The prey density at a specific time t increases with increasing regeneration rate p_S and the reservoir size K_S as being the initial amount of secretion. In this case more prey is defended (i.e. higher $D(S)$) which leads to a lower loss due to predation (i.e. lower $F(B,S)$).
- However, the costs for maintaining the reservoir and producing secretion considerably decrease the prey density when regeneration rate p_S and the reservoir size K_S are very large.
- The prey density at a specific time t increases with decreasing transferring constant e_S as the prey can defend against more predator attacks without regenerating secretion. Hence, more prey is defended (i.e. higher $D(S)$, cp. Eq.(3.13)) which leads to a lower consumption rate (i.e. lower $F(B,S)$).

Fig. 3.1 shows the functional response (i.e. the consumption rate per predator $F(B,S)$) ((a)-(c)), the prey density ((d)-(f)), and the fraction of defended prey ((g)-(i)) in color code as a function of time and in response to changes in the reservoir size K_S (i.e. initial amount of secretion) ((a), (d), (g)), the transferring constant e_S ((b), (e), (h)), and the regeneration rate p_S ((c), (f), (i)).

Initially, no prey is consumed since all prey is defended (s. Fig. 3.1(a)-(c) and Fig. 3.1(g)-(h)). Thus, at first the predator has to decrease the amount of secretion until $S < \frac{K_S+e_S}{2}$ (cp. Eq.(3.13)) which means that some prey is disarmed and thus consumable (s. Fig. 3.1(a)-(c) and Fig. 3.1(g)-(h)). The time until the predator has disarmed some prey increases with increasing regeneration rate p_S (s. Fig. 3.1(c), (i)), increasing reservoir size K_S (s. Fig. 3.1(a), (g)), as being the initial amount of secretion, and with decreasing transferring constant e_S (s. Fig. 3.1(b), (h)), since this increases the number of attacks the prey can defend against without regenerating secretion. Consequently, the time until all prey is consumed also increases with increasing regeneration rate p_S (s. Fig. 3.1(f)) and reservoir size K_S (s. Fig. 3.1(d)) and with decreasing transferring constant e_S (s. Fig. 3.1(e)).

The costs for secretion become visible when the regeneration rate p_S and the reservoir size K_S are large, since prey density decreases although all prey is defended and thus no prey is consumed by the predator (s. Fig. 3.1(c), (f), (i) and Fig. 3.1(a), (d), (g), respectively).

When the transferring constant e_S is very small ($e_S < 15\,\text{ng}$), it has no impact on the prey density anymore (s. Fig. 3.1(e)) as secretion is faster reproduced than released. Hence, all prey is defended (s. Fig. 3.1(h)) and the prey density is determined by metabolic losses.

These results come up to our expectations formulated in the beginning of this section. Hence, we conclude that our model is appropriate.

3.5.2 Comparing different defense strategies

On short time scales, the prey can pursue two strategies in order to reduce its vulnerability:

1. Having a large secretion reservoir and thus the possibility to accumulate a large amount of secretion during an attack-free period.

2. Being able to fast regenerate secretion (i.e. a high p_S).

Since having a large reservoir K_S or a high regeneration rate p_S incur metabolic costs, there is a trade-off between investing in them (s. Eq.(3.19)). We assume that the prey invests a fixed amount of energy in defense, such that metabolic loss caused by defense is constant. Hence, the reservoir size can only be increased by decreasing the regeneration rate and vice versa. In this section, we investigate which strategy is the best under varying conditions, namely varying predation pressure and varying total metabolic costs (i.e. α_B) which are assumed to be caused by differing external influences such as temperature or stressful environments. Hence, an increase in the respiration rate α_B affects the basal respiration rate κ, as well as the cost factors concerning the reservoir size ϑ and the regeneration rate η to the same extent, i.e. by the same scaling factor. For a given α_B, we then distribute the available energy between regeneration rate p_S and reservoir size K_S according to Eq.(3.19). Furthermore, we compare the results to the situation when prey is not able to defend itself, i.e. the regular Holling Type II predator-prey system as described in Section 2.1. In order to value the different strategies, we use the lifetime of the prey population, which we define as the time until one prey individual is left, i.e. $B(t) = \frac{1}{A} = 0.05\,\frac{1}{\text{cm}^2}$. The value for prey density of one individual is inspired by experiments (Heethoff and Rall, 2015).

Fig. 3.2 shows the lifetime of the prey population in dependency of the regeneration rate p_S and the corresponding reservoir size K_S for (a) different predator densities P with $\alpha_B = 0.005\,\frac{1}{\text{h}}$ and (b) different respiration rates of the prey α_B with $P = 0.025\,\frac{1}{\text{cm}^2}$. Hence, the solid line in (a) corresponds to the dashed line in (b). In (c), we show the extreme case of low predator densities P and a high respiration rate $\alpha_B = 0.01\,\frac{1}{\text{h}}$. The horizontal lines in pastel colors mark the lifetime of a prey population that is not able to defend against predator attacks, i.e. $K_S = p_S = 0$.

There are two scenarios why a prey population having no defense mechanism survives longer than a prey population that is able to defend against predator attacks:

1. When the reservoir size and thus the initial amount of secretion of the latter is smaller than the amount of secretion to defend against a single attack e_S (s. Fig. 3.2(a), (b)).

2. When the predator density is low and the costs for defense are high (s. Fig. 3.2(c)).

In the first case, the prey is effectively undefended, but has to take the costs for the ability of fast recovering secretion; in the latter case, the costs for defense exceed the predation loss decrease due to the low predator density. The survival time does not depend on the defense strategy when the costs for defense are high and $K_S > 25\,\text{ng}$ (s. Fig. 3.2(c)). In this case, the metabolic losses are much larger than the losses due to predation which become negligible such that different defense strategies become equally effective. Consequently, prey species that do not have to take the additional costs for defense survive longer when predator density is very low.

When the predator density P and the respiration rate α_B are low, the prey maximizes its lifetime by investing in high regeneration rates p_S although this includes low reservoir sizes K_S (s. Fig. 3.2(a), (b)). In this case, the disarming dynamics are slow enough and the costs for defense are low enough such that the prey can benefit from a large regeneration rate p_S. Otherwise, the prey survives longer by fully investing in a large reservoir (i.e. a large initial amount of secretion), although this includes that the reservoir cannot be refilled (i.e. $p_S = 0$) (s. Fig. 3.2(a), (b)). This is the case because the costs for regenerating secretion fast enough become too high or

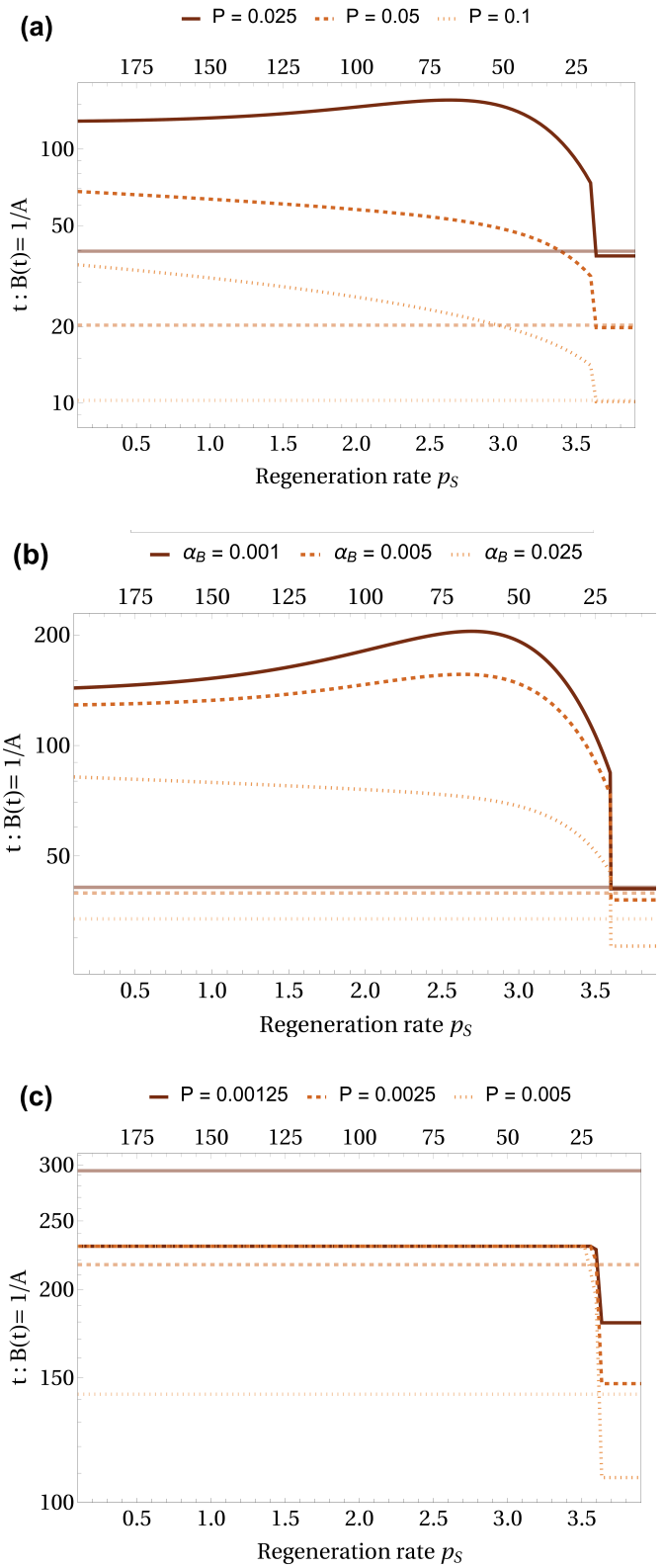

Figure 3.2.: Time until the prey population is reduced to one individual as a function of the reservoir size K_S and the regeneration rate p_S. The total metabolic loss is kept constant such that the reservoir size can only be increased by decreasing the regeneration rate and vice versa. In (a), predator density P is varied with a fixed respiration rate $\alpha_B = 0.005\,\frac{1}{\mathrm{h}}$; in (b), the respiration rate α_B is varied with fixed predator density $P = 0.025\,\frac{1}{\mathrm{cm}^2}$; in (c) we show the extreme case of low predator densities P and a high respiration rate $\alpha_B = 0.01\,\frac{1}{\mathrm{h}}$.

because the attack rate is too high to refill the reservoir fast enough (taking the costs for producing secretion into account).

These results do not include that prey evolves a zero regeneration rate in nature, but that the conditions in experiments do not correspond to those in natural systems. When attack episodes are shorter, for instance because prey is able to hide from predators, the time for regenerating secretion is longer and prey can also benefit from a non-zero regeneration rate.

3.6 Long-term behavior

In this section, we investigate the long-term behavior of our predator-prey model. We tackle three main questions, namely:

- Which effect does reducible defense have on a predator-prey system?
- Under which conditions is it better to invest in defense and under which conditions is it better to invest in offspring?
- Under which conditions is coexistence of predator and prey possible?

In order to do this, we calculate the stable attractor of our dynamical system described by Eq.(3.17) (cp. Section 3.2). This means that starting from some initial condition the system would settle to this attractor since there is only one stable attractor with our choice of parameter values. We thus choose a mean-field like approach, where predator-prey encounters and attack frequencies are described by averaged rates, neglecting their episodic nature. As discussed in Section 3.3, the prey densities are typically lower in nature than in experiments such that we use a carrying capacity of $K_B = 0.04\ \frac{1}{\text{cm}^2}$ (s. Table 3.1) in this section (Binzer et al., 2012).

We focus on the regeneration rate of secretion p_S in order to investigate the impact of reducible defense on the predator-prey system. The regeneration rate p_S and the reservoir size K_S have a similar impact on the system in the long-term limit (s. Eq.(3.17)), but see Fig. C.1 in Appendix C for clarification. As the regeneration of secretion includes metabolic costs (cp. Eq.(3.14)) and thus reduces the growth rate to an effective one (cp. Eq.(3.16)), there is a trade-off between investing in defense or offspring.

Fig. 3.3 shows the (a) prey density, (b) predator density, and (c) the fraction of defended prey at the stable fixed point in color code in response to changes in the regeneration rate p_S and its cost factor η. The white region indicates where the predator goes extinct. For $p_S = 0$, all prey is undefended and thus represents the results for a regular Holling Typ II functional response.

The predator and the prey can coexist when the density of undefended prey, $(1 - D(S))B$, is high enough to provide a sufficing amount of food (cp. Eq.(3.8) and (3.9)). This is the case

1. when the prey density B is not too low, hence when the metabolic losses due to defense are not too high, or
2. when the fraction of undefended prey $(1 - D(S))$ is low, hence when the regeneration rate is not too high.

Consequently, prey and predator can coexist when a given regeneration rate p_S includes adequate costs such that ηp_S is small.

When the costs for regenerating secretion are high ($\eta > 0.1$), prey density decreases with increasing regeneration rate p_S as indicated by the color change from lighter to darker color in Fig. 3.3(a). The prey thus benefits from investing in offspring and a prey population that is not able to defend against predator attacks (i.e. $p_S = 0$) is more abundant than one that has evolved reducible defense. This is the case since the costs for fast refilling the reservoir exceed the benefits of a lower consumption rate due to a higher fraction of defended prey (s. Fig. 3.3(c)). The predator density also decreases with increasing regeneration rate p_S when $\eta > 0.02$ (s. Fig. 3.3(b)) since prey density is lower (when $\eta > 0.1$) and less prey is undefended (s. Fig. 3.3(c)).

However, the prey benefits from a large regeneration rate p_S and thus from investing in defense when the costs for refilling the secretion reservoir are low ($\eta < 0.1$) (s. Fig. 3.3(a)) as illustrated by the color change from darker to lighter color with increasing p_S in Fig. 3.3(a). In this case, more prey is defended (s. Fig. 3.3(c)) and less prey is consumed by the predator. Interestingly, the predator density also increases with increasing regeneration rate p_S when the costs for defense are very low ($\eta < 0.02$). This implies that the consumption rate increase due to

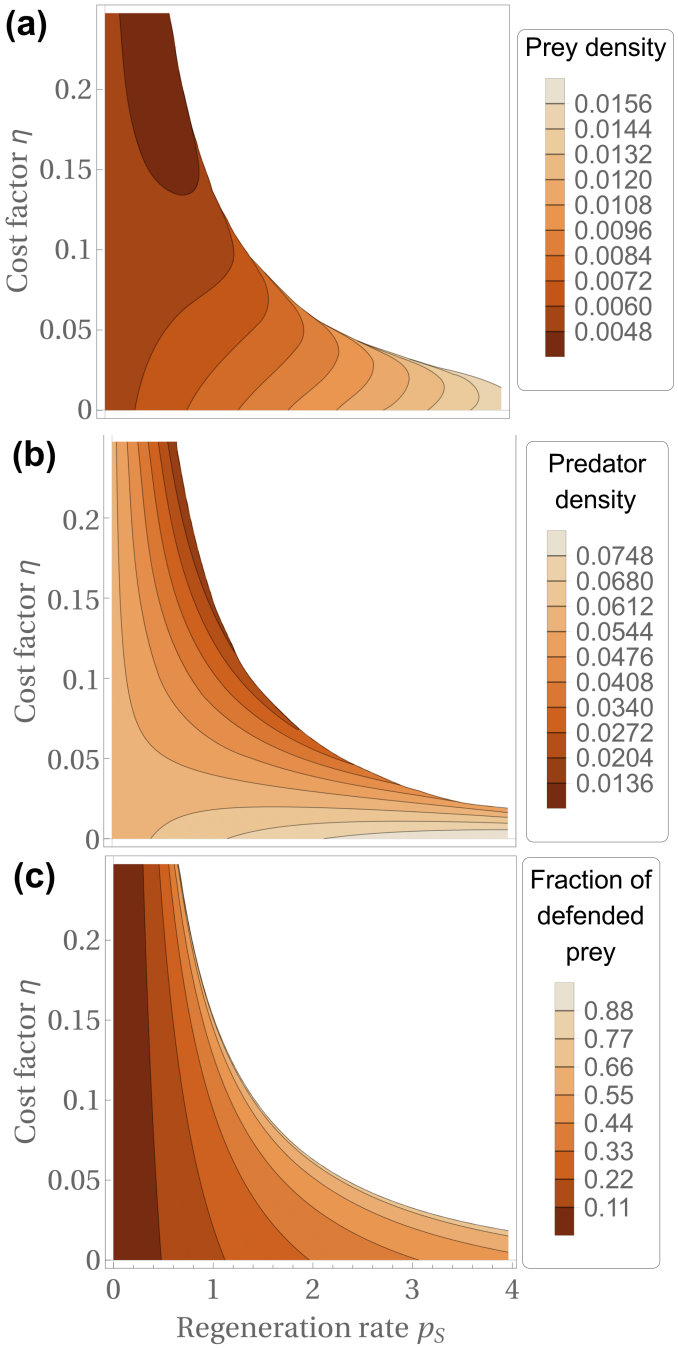

Figure 3.3.: (a) Prey density, (b) predator density, and (c) the fraction of defended prey at the stable fixed point displayed in color code as a function of the regeneration rate p_S and its cost factor η. The white region indicates where the predator goes extinct.

the higher prey density is larger than its decrease due to the higher fraction of defended prey. Consequently, both predator and prey populations can become more abundant when the prey is able to defend against predator attacks via reducible defense (i.e. $p_S > 0$) than in a common predator-prey system as described in Section 2.1.

When the regeneration rate is low ($p_S < 2$), the prey density decreases with increasing cost factor η (s. Fig. 3.3(a)) due to the increasing metabolic loss. As a consequence, predator density also decreases with increasing cost factor η (s. Fig. 3.3(b)). However, when the regeneration rate is high ($p_S > 2$), prey density first decreases with increasing costs factor η, but increases for further increasing η as indicated by the color change from lighter to darker and back to lighter color. The reason why the prey benefits from higher costs for defense is that the predator density decreases with increasing cost factor η. This indicates that the decreased consumption rate outweighs the increased metabolic loss due to higher η.

The predator density has a crucial impact on the optimal investment in defense. In order to distill this impact, we calculate the attractor of the prey density for a fixed predator density P in dependency of the regeneration rate p_S and its cost factor η (s. Fig. 3.4). We consider a (a) small, (b) intermediate, and (c) high predator density. The black region indicates where the prey goes extinct.

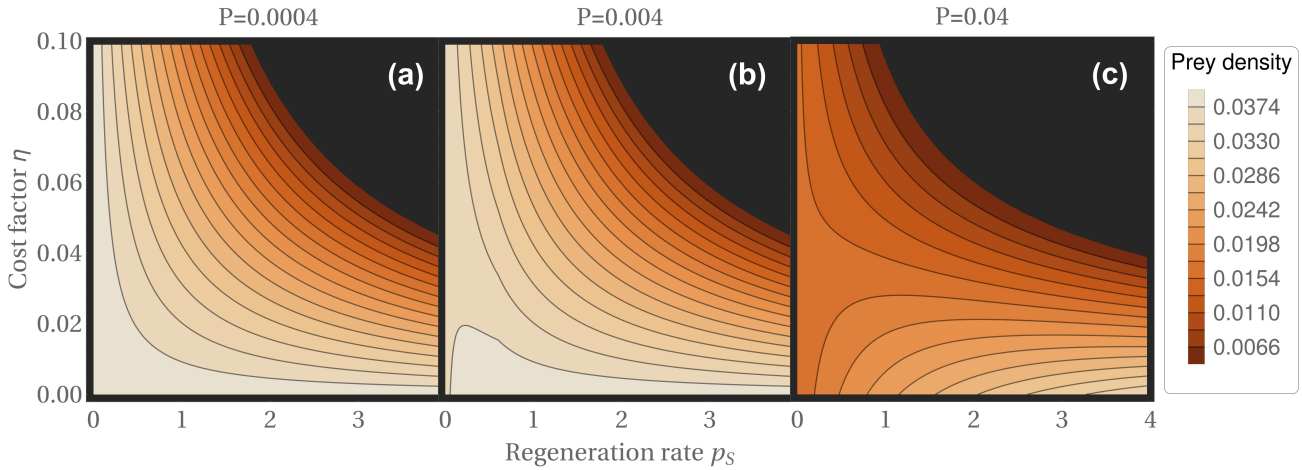

Figure 3.4.: Prey density as a function of regeneration rate p_S and its cost factor η, with the predator density fixed at (a) a small, (b) intermediate, or (c) large value. The black region indicates that prey goes extinct.

As the predator density is fixed, the prey density decreases with increasing costs for defense in this case independently of the regeneration rate p_S and the value of predator density P. When the predator density is low (s. Fig. 3.4(a)), the prey density decreases with increasing regeneration rate p_S as indicated by the color change from lighter to darker color under the assumption of a non-zero cost factor η. The prey thus benefits from investing in offspring since predator attacks happen too infrequently to take the costs for defense. For a higher predator density (s. Fig. 3.4(b)), it becomes beneficial to invest in a low regeneration rate ($p_S \approx 0.3$) when the costs for defense are low ($\eta < 0.02$). In the case of a high predator density (s. Fig. 3.4(c)), the prey benefits from investing in high regeneration rates p_S as long as the costs for defense are not too high ($\eta < 0.03$). This means that the loss caused by predation and thus the potential benefit of defense is high enough to take the costs for defense.

3.7 Summary of major findings

Regarding our research questions (s. Section 3.4), we want to highlight some central findings of this chapter:

- It is beneficial to invest in defense when predator density is not too low and the costs for defense are not too large, both in the short and long time investigation.
- When attacks happen in episodes separated by long recovery times, it is better to invest in the ability of fast refilling the reservoir when both predator density and costs for defense are low. Otherwise, the prey benefits from a large reservoir.
- On long time scales, the prey can benefit from larger costs for defense when this leads to a considerable decrease in predator density.

- Both the prey and the predator can benefit from defense via an increased abundance when the costs for defense are low on long time scales.
- Predator and prey can coexist when the investment in defense and its costs are not too large.

In the next section, we will discuss our model and these central findings.

3.8 Discussion

In this section, we extended the predator-prey model by the feature that prey is able to defend against predator attacks. More precisely, we considered reducible, reservoir-based defense which means that the prey stores secretion in a reservoir which is partly released in response to a predator attack and bioenergetically refilled between attacks. As mentioned in the introduction of this chapter, reducible defense is widespread among invertebrates (Eisner, 2003; Eisner et al., 1961; Johnson et al., 2006b) and although several studies gave evidence to suggest that other defense mechanisms increase the diversity, stability and/or abundance in an ecological system (Vos et al., 2004a,b; Abrams and Walters, 1996; Ruxton and Lima, 1997; Bohannan and Lenski, 1999; Genkai-Kato and Yamamura, 1999), there are little studies that investigated the impact of reducible defense on an ecosystem. Heethoff and Rall (2015) proposed a predator-prey model that considered reducible defense of the prey, however, the study focused on short time scales in order to compare the results to experimental findings. In this study, we proposed a predator-prey model that includes reservoir-based defense of the prey and investigated both the short and long time behavior of this model.

In order to incorporate reservoir-based defense in the predator-prey model, we modified the functional response by taking into account that the predator does not only spend time for capturing and handling (undefended) prey, but also for disarming defended prey. Hence, the maximal ingestion rate includes an additional term which describes the time wasted for unsuccessful attacks on defended prey. The expression that we found is similar to those assumed in (Heethoff and Rall, 2015)[5]. Additionally, we took into account that maintaining and refilling the reservoir includes metabolic costs such that there is a trade-off between investing in offspring or defense. Furthermore, we formulated an additional equation which models the average amount of secretion per prey out of which we determined the fraction of defended prey. These equations are based on a mean-field like approach, but we validated our expression for the fraction of defended prey by performing stochastic, individual-based simulations (s. Appendix B).

In a first step, we focused on the behavior of our model on short time scales as investigated in typical experiments (Heethoff et al., 2011; Brückner et al., 2016; Heethoff and Rall, 2015). This means that we distill the effect of the predator-prey interaction, i.e. feeding and disarming prey. The predator density is kept constant over the simulation time and the reservoirs are assumed to be initially completely filled as in the experiments (Heethoff et al., 2011; Brückner et al., 2016; Heethoff and Rall, 2015). On this time scale, there is a trade-off between investing in a large reservoir or in the ability to fast refill the reservoir as both features include metabolic costs. We find that the size of the reservoir is the crucial feature to maximize the lifetime of the prey. The prey only benefits from the ability to fast regenerate secretion when predator attacks are rare, such that the prey has enough time to regenerate secretion, and the costs for producing secretion are low.

Furthermore, we find that the survival time of a prey population is higher when it is able to defend against predator attacks compared to prey species that have not evolved a defense mechanism when (i) the predator density is not too low combined with low or intermediate metabolic costs and (ii) the initial amount of secretion is large enough to repel an attack. Otherwise the prey has to take the high costs for the ability to fast refill the reservoir without benefiting from defense. Indeed, several studies found that inducible (Agrawal, 1998), constitutive (Raatz et al., 2017), and reducible defense (Heethoff and Rall, 2015) reduce the consumption rate leading to a longer survival time in typical experimental setups (Heethoff et al., 2011; Brückner et al., 2016; Heethoff and Rall, 2015). This indicates that these species live in an environment that fulfills the above mentioned conditions. Furthermore, it is intuitive that defense mechanisms only evolve in environments where the predator pressure is not too low and the costs for defense are not too high.

In the second part, we investigated the long-term behavior of our model. When the costs for defense are not too high, we find that the prey can become more abundant when it is able to defend against predator attacks compared to a regular Holling Type II predator-prey system without any defense mechanism. When the costs are low, the predator also benefits from prey defense as the increase of prey density and the resulting higher consumption

[5] Heethoff and Rall (2015) additionally assumed that attacks on undefended prey succeeds with a certain success rate.

rate outweighs the decrease in this quantity due to the higher fraction of defended prey. Hence, the prey and the predator densities are higher when we include reducible defense in a predator-prey system under the assumption of low costs for defense. Indeed, several studies found that the coexistence of vulnerable and invulnerable prey enhances species abundances (Vos et al., 2004b; Abrams and Walters, 1996; Bohannan and Lenski, 1999; McCauley and Murdoch, 1990), but our study is the first that confirmed this for reducible defense.

However, when the costs for defense are high both predator and prey become less abundant by including reducible defense in the predator-prey model. Hence, it is not worth to invest in defense for the prey. Prey density decreases when the costs for defense increase as expected, however, this is only the case when the regeneration rate p_S is low or when the predator density is fixed. When the regeneration rate p_S is high the prey first decreases, but then increases again with increasing costs for defense. The prey can thus benefit from high costs for defense. This is the case as the decrease of the predator density as a consequence of the prey density decrease outweighs the higher costs for defense.

We further investigated the impact of the predator density on the question whether the prey benefits from reducible defense. Here, we assumed a fixed predator density and calculated the prey density in the stable fixed point. In concert to the results on the short time scales, we found that it is only advantageous for the prey to invest in defense when the predator density is not too small and the costs for defense are not too high. Several empirical studies also found that the investment in defense mechanisms depends on their costs (Kasada et al., 2014; Kraaijeveld and Godfray, 1997; van Hulten et al., 2006; Tien and Ellner, 2012). Reasons for an increase in the costs may be that predators are larger or more difficult to deter, a reduced resource availability (Yoshida et al., 2004; Tien and Ellner, 2012) or a stressful environment (Bergelson and Purrington, 1996; Brodie, 1999; Siemens et al., 2003) although there are counterexamples (Siemens et al., 2002). Furthermore, Kasada et al. (2014) found that preys especially evolve defense when the cost for defense is not too high, or when the predator consumption rate is not too low in concert with our findings.

In a nutshell, we showed that reducible defense is beneficial for the prey when its costs are not too high and the predator density is not too low. Furthermore, reducible defense can increase both predator and prey density.

Finally, let us emphasize that our model also applies for a predator-prey system, where the predator needs several attacks to injure the prey severely enough to make it consumable (i.e. non-lethal predator attacks). In this case, S describes the health level of the prey and p_S the healing rate of the prey (cp. Eq.(3.10)).

4 Impact of stochastic migration on species diversity in meta food webs

The spatial scale has considerable impact on an ecosystem (Dey and Joshi, 2006; Hauzy et al., 2010; Holyoak and Lawler, 1996; Molofsky and Ferdy, 2005; Plitzko and Drossel, 2014; Gravel et al., 2016). In this chapter, we investigate several detached living environments, which we will call habitats or patches. We consider that each of these patches contains a food web, i.e. multiple interacting species[1]. Such systems are also called metacommunities (Holyoak et al., 2005) or meta food webs. Between these patches, species can move and we investigate the impact of this migration[2] on the stability and diversity (i.e. the number of species) of the ecological system.

Several studies found that migration enhances species survival and coexistence in both empirical and theoretical studies (Dey and Joshi, 2006; Hauzy et al., 2010; Holyoak and Lawler, 1996; Molofsky and Ferdy, 2005; Plitzko and Drossel, 2014) since species that went extinct for some reason on one patch can reinvade from neighboring patches. This is the so-called "rescue effect" (Plitzko and Drossel, 2014). Furthermore, the increased number of phase space dimensions allows for new attractors and thus the coexistence of species that cannot coexist on isolated patches (this effect is called "dynamical coexistence" (Plitzko and Drossel, 2014)). However, most of these studies consider simple local systems, which means that the patches contain the populations of one species (Dey and Joshi, 2006; Molofsky and Ferdy, 2005) or a predator-prey system (Hauzy et al., 2010; Holyoak and Lawler, 1996). Plitzko and Drossel (2014) confirmed the diversity enhancing effect of migration for complex food webs each containing up to 60 species on up to 20 patches.

The diversity increase due to migration is strongest for intermediate migration rates as the patches synchronize when migration rates are high (Plitzko and Drossel, 2014; Hauzy et al., 2010; Gravel et al., 2016). This means that the population densities of a species reach their minimum on all patches at the same time, such that the species goes extinct on all patches at the same time when population densities become too low. Synchronization thus increases the risk of global extinction of a species. In the limit of very high migration rates, all patches are fully synchronized and behave as one large patch (Plitzko and Drossel, 2014).

As most theoretical studies used deterministic equations to determine the effect of migration (Plitzko and Drossel, 2014; Hauzy et al., 2010), they found that migration does not affect species survival and coexistence when migration rates are low as the immigrating biomass is too low to ensure species' survival. Deterministic modelling is, however, an idealization that allows less computational effort and that is appropriate when populations are large and migration rates are not too low (Allen, 2010; Kurtz, 1970). When these conditions are not fulfilled, deterministic modelling is inappropriate as stochastic effects become important. Stochastic effects can considerably change the dynamics of a system compared to its deterministic version, for instance, they can lead to extinction, to shifts of equilibria and bifurcations, or to periodic oscillations (Black and McKane, 2012; Grima, 2010; McKane and Newman, 2005). Furthermore, several empirical studies suppose that the origin of their findings are stochastic effects (Antonovics and Edwards, 2011; Higgins et al., 1997; Krkošek et al., 2011).

Stochasticity was included in several metacommunity models in several different ways. For instance, the impact of environmental fluctuations (Lande, 1993), fluctuations of interactions (Keeling and Gilligan, 2000), and random fluctuations in local birth and death rates (Lande, 1993) (also known as demographic stochasticity (Yaari et al., 2012)) on species' persistence were investigated. These studies found that such fluctuations can increase species coexistence, but also the risk of extinction. Several studies use individual-based models where time evolution is a stochastic process based on reaction and transition rates (Alonso and McKane, 2002; Black and McKane, 2012; Economo and Keitt, 2008; Ross et al., 2008; Ross, 2006; Yaari et al., 2012). As individual-based models are computationally very expensive, they are mostly used to model simple local systems consisting only of a few species. For instance metapopulations (i.e. one species on several patches) or predator-prey systems (i.e. two species on several patches) (Alonso and McKane, 2002; McKane and Newman, 2005; Simonis, 2012) have been investigated, whereby neutral models (Hubbell, 2001) mark an important exception (Economo and Keitt, 2008, 2010).

[1] See Section 4.1.1 for details.

[2] We will use the term migration to describe the steady biomass flow between patches. Often, this term is used to describe periodic movements, for instance depending on the season as bird migration (Clobert et al., 2012). To comply with our paper (Thiel and Drossel, 2018), this part of the thesis is based on, we do not use the term migration in this sense.

Indeed, Economo and Keitt (2008, 2010) used a spatial explicit neutral model to investigate the impact of the migration rate on α- (i.e. local[3]) and γ- (i.e. regional[4]) diversity and they found, similarly to deterministic models, that the local diversity increases with increasing migration rates. However, neutral models consider species that occupy similar positions in a food web[5], e.g. all species are primary producers such as plants. However, in nature, consumer-resource interactions, and thus species that have different positions in the food web, often have an important impact on an ecosystem. Hence, investigating the impact of stochastic migration on an ecological system consisting of several patches each containing a complex food web represents an important contribution for understanding the impact of migration.

In this chapter, we fill this gap. We embed stochastic migration in our deterministic equations to describe local dynamics of a metacommunity and compare the results with a completely deterministic model. With this approach, we distill the effect of stochastic migration. In particular, we are interested in the characteristics of the species that mainly benefit from migration and in the limit when migration events happen infrequently enough that the system can reach an attractor between two migration events. We will call this limit the adiabatic limit.

This study was created in collaboration with Barbara Drossel and was published in the "Journal of theoretical biology" with the title "Impact of stochastic migration on species diversity in meta-food webs consisting of several patches" (Thiel and Drossel, 2018). Barbara Drossel provided general advice for this study and especially for the investigation of the adiabatic limit. Everything else, i.e. the implementation of the model, the simulations, the interpretation of the results, and the draft of the paper manuscript were done by the author of this thesis. Concerning the latter, Barbara Drossel also provided essential linguistic revision.

4.1 Basics

In this section, we introduce the basics required to model stochastic migration in metacommunities, i.e. a spatial web consisting of several connected patches, each containing a complex food web. In order to do this, we need to introduce three more aspects, namely,

- a model to construct realistic complex food webs, i.e. the static structure,
- an expansion of the simple consumer-resource population dynamics Equation(2.1) to complex food webs, and
- an equation to model migration (as a stochastic process).

We will focus on these points in the following.

4.1.1 What is a food web?

A food web is an ensemble of interwoven consumer-resource interactions and thus consists of several species and their interactions. In this chapter, we focus on predator-prey interactions. In the following, we introduce some technical terms concerning food webs.

Representation as graphs and connectance

Food webs can be represented as graphs where predator-prey interactions are displayed as directed edges between nodes, which characterize different species as illustrated in Fig. 4.1. The direction of the edges depicts the energy flow[6] in the food web (Allhoff, 2015; Bornholdt and Schuster, 2006).

The presence of links can be represented as ones in the adjacency matrix A while zeros mark the absence of links. If cannibalism is excluded $S(S-1)$ links are possible considering S species/nodes. The connectance C describes the proportion of realized links, i.e.

[3] This means the number of species on each patch averaged over all patches.

[4] This means the number of species that survive in the whole system, i.e. on any patch.

[5] The technical term here is that the considered species are on the same *trophic level*. We introduce the trophic level in detail in Section 4.1.1

[6] Here, a species is considered as an energy processor that gains energy from its environment, for example due to predation (Yodzis and Innes, 1992). Then, the species converts a proportion of this energy into biomass.

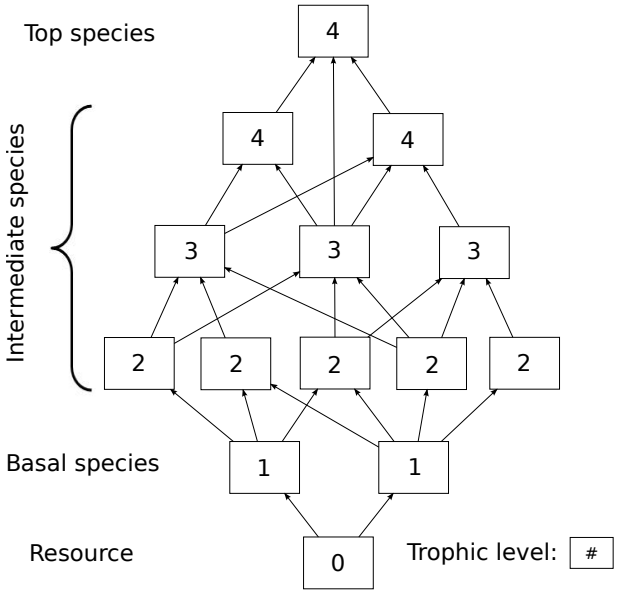

Figure 4.1.: Schematic representation of a food web. The direction of the edges depicts the energy flow through the food web.

$$C = \frac{L}{S(S-1)}, \tag{4.1}$$

where L is the number of actual links.

Trophic level

We consider an external energy pool, which represents the food for all species that have no prey. In the following, we will refer to this external energy pool as resource (cp. Fig. 4.1). As the edges mark the energy flow through the food web and the transformation from consumer's diet into consumer's biomass requires energy, the number of edges to reach the resource is an important measure to characterize the species in a food web (Williams and Martinez, 2004a). This measure is called the trophic level of a species. In complex food webs, however, this definition is ambiguous since there may be multiple paths requiring differing number of edges to reach the resource, i.e. different number of transformation from consumer's diet into consumer's biomass. In this thesis, we use the definition of the trophic level as the *shortest* path to reach the resource (Allhoff, 2015; Plitzko and Drossel, 2014) as illustrated in Fig. 4.1.

All species with trophic level one, i.e. that feed directly from the resource, are called basal species. While top species include all species that do not have any predator, intermediate species cover all species that have at least one predator and one prey species (Bornholdt and Schuster, 2006). Consequently, top species can have the same trophic level as intermediate species (cp. Fig. 4.1).

4.1.2 How to construct a realistic food web?

It is non-trivial to construct realistic food webs. In this section, we explain why this is the case by providing a brief overview of the first attempts. Furthermore, we introduce the model that we used for our investigations.

First attempts

Inspired by the work of Erdős and Rényi (1976), random graphs were used in the first attempts to construct realistic food webs (Cohen, 1977; Pascual et al., 2006). Hence, any link between two species is realized with a probability $P = C$, where C describes the desired connectance of the graph. However, these random networks could not display

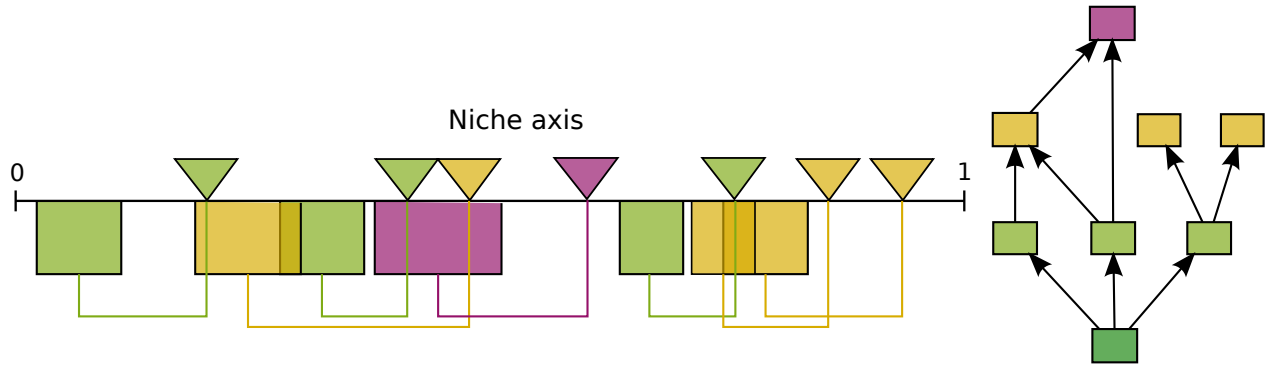

Figure 4.2.: Schematic representation of the construction of food webs with the niche model. The triangles show the niche values of the species, while the rectangles illustrate the feeding ranges of the species. The resulting food web is depicted in the right side of the figure. The basic idea of this figure was created in cooperation with Michaela Hamm.

the high stability of complex food webs in nature (May, 1972). Thus, the idea arises that natural food webs have a special topology that enables the higher stability of complex webs. A model to construct realistic food webs may need special, nature-inspired rules (Jacquet et al., 2016).

One of the first realizations of such a model was the cascade model (Cohen et al., 1985) that takes into account that species often feed on species that have a smaller body mass. Here, a random number $r \in [0,1]$ is assigned to each species that can be interpreted as a body mass and it is assumed that species can only feed on species that have a lower random number (i.e. body mass) (Cohen et al., 1985; Pascual et al., 2006). Such a possible link is then realized with a probability $P = 2C$, where C is the connectance of the graph as defined in Eq.(4.1) (Cohen et al., 1985; Pascual et al., 2006). Hence, this model excludes cannibalism and provides a clear body mass inspired structure. Indeed, this model can construct food webs that have similar key measurements as natural food webs, as for instance the numbers of intermediate species and the number of links from basal to intermediate, intermediate to intermediate, and intermediate to top species (Cohen et al., 1985; Pascual et al., 2006).

Niche model

In 2000, Williams and Martinez (2000) provided a new model, called the niche model, that achieves even better results than the cascade model. In contrast to the cascade model, species can additionally feed on species with a comparable or slightly larger mass than its own. More precisely, a species is defined by three key traits, namely a niche value, a feeding center, and a feeding range. The niche value n_i is drawn uniformly from the interval $[0,1]$ and is interpretable as the body mass of the species (in an appropriate unit[7]). A random number $r_i \in [0,1]$ is drawn from a beta-distribution $P(r|1,b) = b(1-r)^{b-1}$, with $b = (1-2C)/2C$ and the connectance C of the food web (Williams and Martinez, 2000). The feeding center c_i is drawn uniformly from the interval $[n_i r_i/2, n_i]$, and the feeding range is defined as $[c_i - n_i r_i/2, c_i + n_i r_i/2]$. The feeding interactions are then determined as follows: all species i with a niche value in the feeding range of species j are a prey of species j. This procedure is illustrated in Fig. 4.2.

The niche model constructs food webs that reflect multiple key properties of natural food webs, such as the food chain length or the fraction of top, intermediate, and basal species (Williams and Martinez, 2000) and, as mentioned above, achieves even better results than the cascade model. Although there are models with more complicated, but also more realistic rules (e.g. (Hoch, 2016)), the niche model provides a very good trade-off between simplicity and realistic results. Consequently, we use this model for our investigation in this chapter.

4.1.3 Population dynamics in a food web

When we know all predator-prey interactions in the food web, the population dynamics equations for a consumer-resource system as defined in Eq.(2.1) can be easily expanded for a whole metacommunity by appropriately sum-

[7] Often, the mass of species i is defined as $m_i = 10^{x n_i}$ with the niche value n_i and the allometric scaling factor x (cp. Section 4.8) (Heckmann et al., 2012).

ming up all predator-prey interactions. Then, the population density N_i^u of species i on patch u evolves over time according to the following equation

$$\begin{aligned}\frac{\mathrm{d}N_i^u(t)}{\mathrm{d}t} =& \lambda_{ij} \sum_{j \in R_i} \frac{a_{ij} f_i^u N_j^u}{1 + \sum_{l \in R_i} a_{il} f_i^u T_h N_l^u} N_i^u \\ &- \sum_{k \in P_i} \frac{a_{ki} f_k^u N_i^u}{1 + \sum_{m \in R_k} a_{km} f_k^u T_h N_m^u} N_k^u \\ &- \alpha_i N_i^u - \beta_i \left(N_i^u\right)^2 + M_i^u \left(\vec{N}_i\right),\end{aligned} \tag{4.2}$$

with $\vec{N}_i = (N_i^1, N_i^2, \ldots, N_i^Y)$, where Y describes the number of patches in the system.

As in the consumer-resource system (cp. Section 2.1), the first two terms describe food ingestion and predation loss using a Holling type II functional response (Holling, 1965). The sets P_i and R_i denote all predators and prey of species i, respectively. The fractional foraging effort f_i^u is the inverse of the number of prey species of predator i and takes into account that a predator with multiple preys needs to split its hunting time. This ensures that species having only one food source, so-called specialists[8], do not have a clear disadvantage compared to generalists having multiple food sources. Specialists and generalists can thus coexist in a food web as observed in natural systems (Lankau, 2007). The third term describes mortality and biomass loss due to metabolism (for instance respiration), while the fourth term is a quadratic loss term describing loss due to disease spreading or limited availability of space for instance for nesting sites; again as in the consumer-resource system (cp. Section 2.1). The last term captures the effect of migration between patches. We explain this term in detail in Section 4.1.4.

Equation for basal species

For basal species, the population dynamics Equation(4.2) simplifies as the constant external resource R represents the only "prey" for basal species, i.e. $f_b^u = 1$. Additionally, the first and fourth term in Eq.(4.2) together describe the logistic growth of a basal species b, i.e.

$$\begin{aligned}\frac{\mathrm{d}N_b^u(t)}{\mathrm{d}t} =& \underbrace{\lambda_b \frac{a_b R}{1 + a_b T_h R}}_{r} N_b^u \\ &- \sum_{k \in P_b} \frac{a_{kb} f_k^u N_b^u}{1 + \sum_{m \in R_k} a_{km} f_k^u T_h N_m^u} N_k^u \\ &- \alpha_b N_b^u - \beta_b \left(N_b^u\right)^2 + M_b^u \left(\vec{B}_b\right) \\ =& r N_b^u \left(1 - \frac{\beta_b}{r} N_b^u\right) - \alpha_b N_b^u + M_b^u \left(\vec{B}_b\right) \\ &- \sum_{k \in P_b} \frac{a_{kb} f_k^u N_b^u}{1 + \sum_{m \in R_k} a_{km} f_k^u T_h N_m^u} N_k^u,\end{aligned} \tag{4.3}$$

such that the competition factor β_b of species b divided by the growth rate r takes the role of the carrying capacity K_B in the consumer-resource model (s. Section 2.1), i.e. in Eq.(2.1). Basal species are thus described by a comparable population dynamics equation as the resource in the consumer-resource model (s. Eq.(2.1).

Transition to biomass densities

In food web ecology, biomass densities are often used instead of population densities. The biomass density B_i describes the accumulated body mass over all individuals of a species i per area, i.e.

[8] More precisely, specialists can be subdivided in oligophagous species that feed on one prey family and monophagous species that consume only a single species. The latter are very rare.

$$B_i = N_i m_i \,, \tag{4.4}$$

with the body mass m_i of an individual of species i. Including Eq.(4.4) in Eq.(4.2) leads to the population dynamics of the biomass density of species i on patch u, i.e.

$$\begin{aligned}\frac{\mathrm{d}B_i^u(t)}{\mathrm{d}t} =& \lambda \sum_{j \in R_i} \frac{\frac{a_{ij}}{m_i} f_i^u B_j^u}{1 + \sum_{l \in R_i} \frac{a_{il}}{m_l} f_i^u T_h B_l^u} B_i^u \\ &- \sum_{k \in P_i} \frac{\frac{a_{ki}}{m_k} f_k^u B_i^u}{1 + \sum_{m \in R_k} \frac{a_{km}}{m_m} f_k^u T_h B_m^u} B_k^u \\ &- \alpha_i B_i^u - \frac{\beta_i}{m_i} \left(B_i^u\right)^2 + M_i^u\left(\vec{B}_i\right) .\end{aligned} \tag{4.5}$$

In our investigation, we want to distill the impact of stochastic migration by neglecting allometric scaling and that species have different body masses. Hence, we assume that

- the area scanned per time interval divided by the body mass m_i is constant, i.e. $a = \frac{a_{ij}}{m_j}$,
- the respiration rate is the same for all species, i.e. $\alpha = \alpha_i$,
- the competition rate divided by the body mass m_i is constant, i.e. $\beta = \frac{\beta_i}{m_i}$, and
- the assimilation efficiency is the same for all species, i.e. $\lambda = \lambda_{ij}$,

such that Eq.(4.5) simplifies to

$$\begin{aligned}\frac{\mathrm{d}B_i^u(t)}{\mathrm{d}t} =& \lambda \sum_{j \in R_i} \frac{a f_i^u B_j^u}{1 + \sum_{l \in R_i} a f_i^u T_h B_l^u} B_i^u \\ &- \sum_{k \in P_i} \frac{a f_k^u B_i^u}{1 + \sum_{m \in R_k} a f_k^u T_h B_m^u} B_k^u \\ &- \alpha B_i^u - \beta \left(B_i^u\right)^2 + M_i^u\left(\vec{B}_i\right) .\end{aligned} \tag{4.6}$$

For our investigation, we use Eq.(4.6) to model the dynamical behavior of a metacommunity. In Section 4.8, we test the robustness of our results when considering allometric scaling.

4.1.4 Migration

In this section, we describe how we model the movement of the species between the patches. In the literature, two terms are used for this movement, namely, migration and dispersal (Clobert et al., 2012). We use the term migration to describe the steady biomass flow between patches. Often, this term is used to describe periodic movements, for instance depending on the season as bird migration (Clobert et al., 2012). To comply with our paper (Thiel and Drossel, 2018), this part of the thesis is based on, we do not use the term migration in this sense.

Deterministic formulation

Migration (or dispersal) is modelled in multiple different versions in the theoretical ecology community ranging from simple "diffusive" migration (Plitzko and Drossel, 2014), which means that the average biomass flow from a patch to its neighbor is proportional to the biomass in that patch, to adaptive migration. The latter means that species move correspondingly to the conditions on the present patch or the surrounding patches (Brechtel et al., 2018; Gramlich, 2018). In this thesis, we consider diffusive migration as in previous studies that may act as a point

of comparison (Plitzko and Drossel, 2014). More precisely, we assume that the biomass density moving from one patch to linked ones is proportional to the number of linked paths such that we assume the following migration term

$$M_i^u\left(\vec{B}\right) = d \sum_{v \in L_u} \left(B_i^v - B_i^u\right), \tag{4.7}$$

when deterministic equations are used (Plitzko and Drossel, 2014). The set L_u includes all patches that are connected to patch u and we denote the proportionality factor as migration strength d.

Stochastic migration

In our study, the migration term is modeled as a stochastic process. When migration rates are small, we thus ensure that the migrating biomass density cannot become arbitrarily small since at least one individual of a species has to move between the patches. Hence, we consider that discrete biomass packages of a fixed size B_{migr} move between the patches. The discrete biomass packages may be interpreted as the biomass of one individual, i.e. its body mass, or the smallest amount of biomass required to represent a reproductive population.

We use the Gillespie algorithm (Gillespie, 1976) for the numerical implementation of stochastic migration. The Gillespie algorithm generates a statistically correct possible solution of a stochastic equation. In the implementation, we first calculate the point in time at which the next migration event takes place and then choose the species which migrates in this event with probabilities proportional to the biomass densities. Finally, we choose the destination patch. Until the point in time of the next migration event is reached and thus its execution, we calculate local population dynamics. After each migration event, we then calculate the point in time of the next migration event and so on. Hence, we alternate between calculating local population dynamics with deterministic equations and executing migration events (cp. Fig. 4.3).

Note, that the biomasses and therefore the selection probabilities can change between the choice of the next migration event and its execution. Hence, the time between two migration events should not be chosen too large in order to ensure that the biomasses cannot change significantly in this time. In all of our investigations, we tested that this has no significant impact on our results.

In order to ensure comparability to deterministic migration, we claim that the parameters of the Gillespie algorithm must be chosen such that the mean time between two migration events is

$$\bar{\tau} = \frac{B_{\text{migr}}}{d} \frac{1}{\sum_{i,u} B_i^u q^u}, \tag{4.8}$$

with the number of links q^u of patch u and the migrating biomass unit B_{migr}. Again, i counts over all species and u over all patches. In Appendix D, we show in detail that this requirement leads to the mean migration rates of

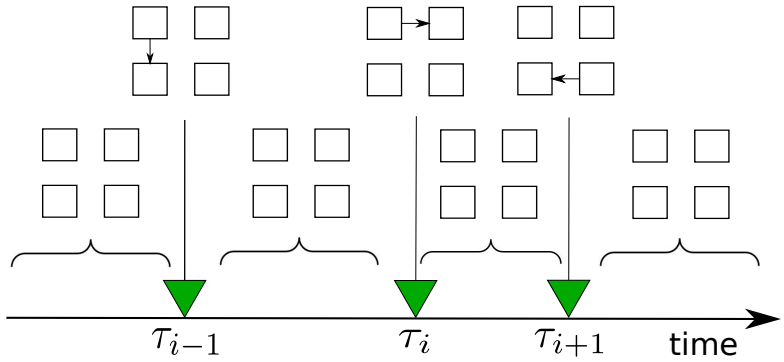

Figure 4.3.: Illustration of stochastic migration. First, we determine a point in time τ_i that identifies the moment of the next migration event. At this point in time the migration event is executed and the migrating biomass unit B_{migr} of a species moves to another patch. Between two migration events, only local dynamics is calculated and no movement between the patches takes place.

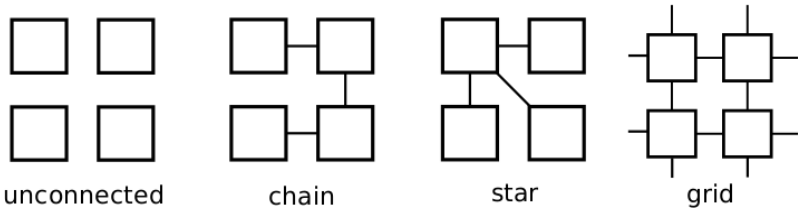

Figure 4.4.: Patch arrangements used in the computer simulations.

Eq.(4.7) in the deterministic limit. With this approach, we can hence model stochastic migration considering different migrating biomass units B_{migr} and mean times between two migration events $\bar{\tau}$, which nevertheless corresponds to the same deterministic model for an appropriate migration strength d.

With this implementation, migration can lead to the extinction of a species on the origin patch when its biomass on this patch is sufficiently small. Since this does not affect the biodiversity of the metacommunity, we only allow migration of species that have a biomass density of

$$B_i^u \geq 2B_{\text{exth}} + B_{\text{migr}}\,, \tag{4.9}$$

with the migrating biomass unit B_{migr} being the discrete biomass package of a fixed size that moves between the patches when a migration event takes place. The extinction threshold B_{exth} is the lowest biomass density a species can have without going extinct. We chose this criterion such that the number of disallowed migration events is small, but the extinction of a species due to emigration happens infrequently enough to be neglected.

As mentioned in the introduction, we are in particular interested in the adiabatic limit, which means that migration events happen infrequently enough such that an attractor is reached between two migration events. In this case, we ensure that the system has reached an attractor before we calculate the time of the next migration event, the migrating species, and the patch of e- and immigration. With this procedure, the probability that a species is chosen for migration is proportional to its biomass in the attractor.

4.2 Setup for the calculations

For our investigation, we construct food webs using the niche model that contain $S = 18$ species including three basal species. Thereby, we exclude cannibalism. Basal species, i.e. species that have no prey, receive their energy from a constant external resource pool R (cp. Section 4.1.3). In order to ensure that different food webs have a similar energy flow through the food web, we only use food webs with an actual connectance that differed by less than 0.1 from the average connectance $C = 0.15$, which we use for the beta-distribution in the niche model (cp. Section 4.1.2; s. Tab. 4.1).

We assume that initially all patches contain the same food web and only differ in the initial biomasses of the species. These are chosen uniformly from the interval $[10^{-7}, 10^{-1}]$, whereby the upper limit of this interval is chosen such that species survival is maximal on an isolated patch (Plitzko and Drossel, 2014). During the simulation, we alternate between calculating local dynamics and executing migration events. After each time step of the solving algorithm, we remove all populations with a biomass below the extinction threshold B_{exth}. We perform the simulation long enough to ensure that the initial phase is over and that the system does not change severely anymore.

For the spatial network, we use three connection topologies which are shown in Fig. 4.4 – the chain, the star, and the grid. The unconnected case serves as a point of comparison.

In this study, we average over 4000 runs, i.e. 4000 different food webs constructed under the constraints named above. For each food web, we determine local and regional robustness averaged over 100 different initial conditions. Local robustness is the fraction of species that survive until the end of the simulation time, evaluated for each patch separately, and then averaged over all patches. For regional robustness a species is counted as a persisting one when it survives on any of the patches. Hence, robustness is also a measure of the diversity (i.e. the number of coexisting species) in the metacommunity.

We vary the migrating biomass unit $B_{\text{migr}} \in \{10^{-5}; 2\cdot 10^{-5}; 4\cdot 10^{-5}\}$, such that it corresponds to multiples of the extinction threshold $B_{\text{exth}} = 10^{-5}$. We further assume that the number of patches varies in $Y \in \{4; 9; 16\}$. The remaining parameters are shown in Table 4.1. They are inspired by empirical studies (Yodzis and Innes, 1992;

Brose et al., 2006b). In order to distill the impact of migration, we choose the size of the constant resource pool high enough to ensure that extinctions are caused by a missing feasibility of coexistence. For the same reason and in order to compare our findings to the work of Plitzko and Drossel (2014), we neglect allometric scaling. In Section 4.8, we however verify that our results also apply when considering allometric scaling.

Table 4.1.: List of parameter values that we use for population dynamics (s. Eq.(4.6)).

Connectance	Attack rate	Assimilation efficiency	Handling time	Respiration rate	Competition rate	Resource size
C	a	λ	h	α	β	R
0.15 ± 0.01	6	0.65	0.35	0.30	0.50	2.5

4.3 Research questions

As in the previous chapter, we start by defining some research questions, that we want to investigate in this chapter. These are:

- Do small migration rates suffice to observe the stabilizing effect of migration (when migration is modelled as a stochastic process)?
- Does the extent of a stabilizing effect of stochastic migration depends on the patch arrangement, the number of patches, or the size of the migrating biomass unit?
- Do we observe both the rescue effect and dynamical coexistence?
- Species of which trophic level are the main profiteers of the observed effects?
- What can happen in the adiabatic limit of infrequent migration events?

In order to tackle these questions, we first analyze the impact of stochastic migration on local and regional robustness, and then discuss the contribution of each trophic level and of the different possible survival mechanisms. Thereafter, we will investigate the adiabatic limit in detail and the impact of allometric scaling.

4.4 Local and regional robustness

Fig. 4.5 shows the local (orange) and regional robustness (red) of the metacommunity as a function of the logarithm of the migration strength d and in dependency of different migrating biomass units B_{migr} (first row), topologies of the spatial web (second row), and number of patches (third row). The basic set-up that is considered in all three rows is a chain of four patches and a migrating biomass unit of $B_{\text{migr}} = 2 \cdot 10^{-5}$. For comparison, we marked the adiabatic limit in each panel as dashed horizontal lines and local and regional robustness in the deterministic limit as dotted lines. Hence, in the limit of very small migration strengths d, the solid lines approximate the dashed lines, and in the limit of large migration strengths d, the solid lines reach the dotted lines. We tested that this is true and show here only the range of d between these limits for ensuring a clearer graphical representation of the interesting observations.

Using stochastic migration, local and regional robustness are lowest in the adiabatic limit and increase with increasing migration strength d. As a species is count as a persisting one when it survives on any patch for regional robustness, its increase means that additional species persist with increasing migration strength, i.e. species that never survive on any patch when patches are weaker connected. The increase of local robustness, however, shows that the metacommunities contain more species in average. Furthermore, local and regional robustness approach each other with increasing migration strength d, which means that the patches become more similar in the species they contain.

Local and regional robustness in the deterministic limit are lower than the corresponding values obtained with stochastic migration for the whole migration strength interval we considered. As expected the results of stochastic migration and the deterministic limit are most similar for the highest migration strength we considered (i.e. $d =$

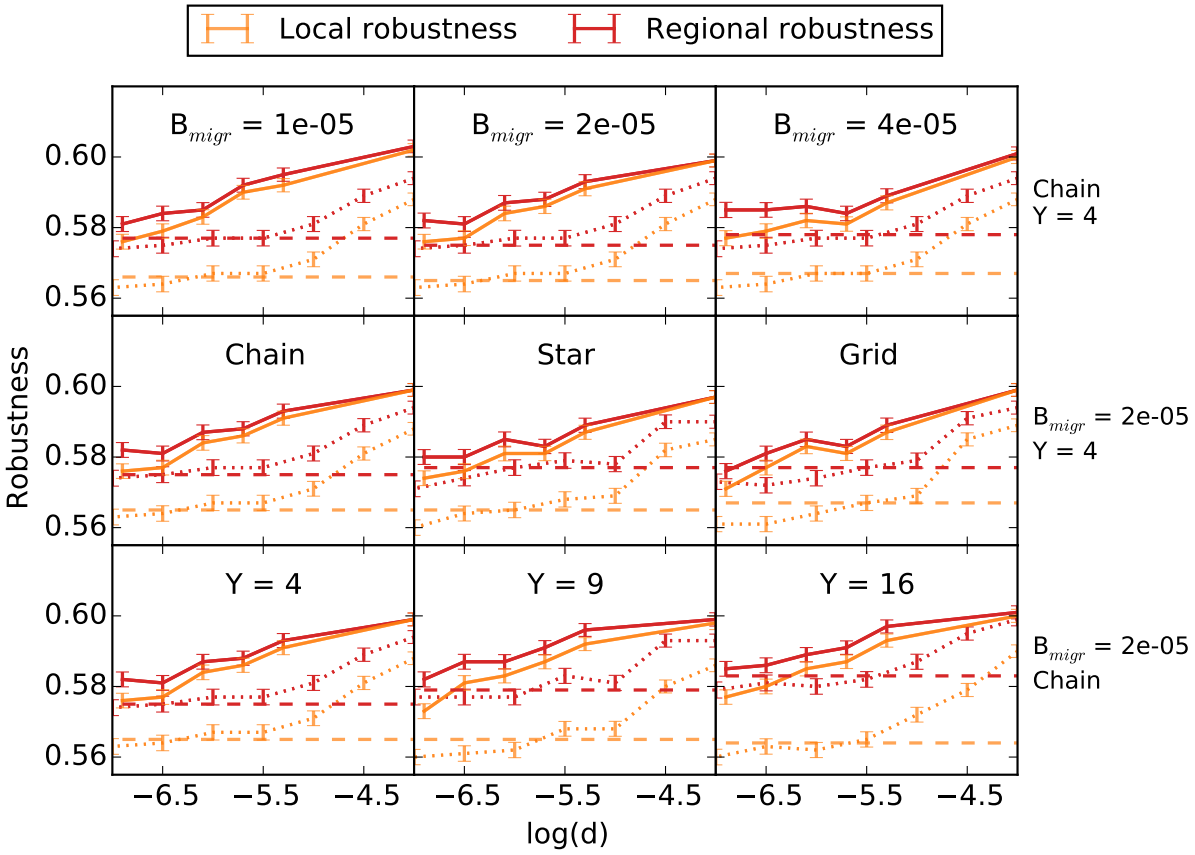

Figure 4.5.: Robustness as a function of the logarithm of the migration strength d, using different migrating biomass units B_{migr} (first row), topologies (second row) and numbers of patches Y (third row). The dashed lines mark the adiabatic limit, the dotted lines show the deterministic limit for local (orange) and regional robustness (red), respectively.

10^{-4}) since deterministic modelling of migration is a good approximation when migration rates are not too low. In the limit of small migration strengths (i.e. $d = 10^{-7}$), local and regional robustness in the deterministic limit are lower than in the adiabatic limit. As the patches are quasi unconnected when considering such a low migration strength d in the deterministic limit, this indicates that the system benefits from stochastic migration in form of a higher robustness independent of the migration strength, i.e. even in the adiabatic limit.

The topology of the patches has no significant impact on the robustness of the metacommunity, but local and regional robustness decrease with increasing migrating biomass unit B_{migr} and with decreasing number of patches Y. In the adiabatic limit, the migrating biomass unit B_{migr} has, however, no impact on local and regional robustness, while regional robustness increases with increasing number of patches Y. This indicates that the probability that species survive on some patch increases with increasing Y, which can then spread across the patches when the migration strength d is high enough. In the following subsections, we investigate these observations in detail.

4.5 Contribution of different trophic levels to the robustness increase

First, we analyze which trophic levels mainly lead to the robustness increase. In order to do this, we calculate the local robustness when stochastic migration is possible and subtract the local robustness when patches are unconnected for each trophic level separately. Fig. 4.6 shows this robustness increase caused by migration in dependency of the logarithm of the migration strength d evaluated separately for each of the first three trophic levels and for different migrating biomass units B_{migr}. The impact of migration on the higher trophic levels is not shown here as it is very low and thus negligible. The total robustness increase summed up over all trophic levels is shown in the top panel of Fig. 4.6.

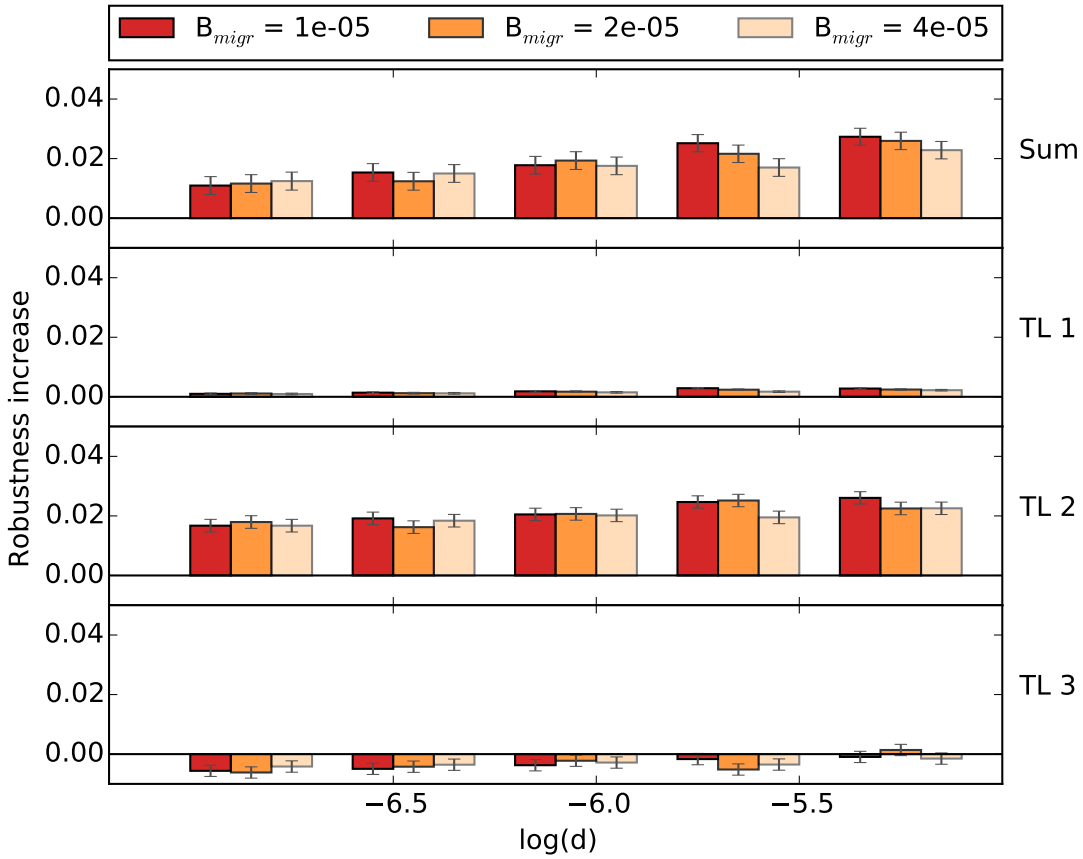

Figure 4.6.: Robustness increase due to connecting four separate patches to a chain, plotted against the logarithm of the migration strength d, and evaluated separately for each of the first three trophic levels (TL), for different migrating biomass units B_{migr}. The error bars in the figure were calculated via error propagation using the standard deviations for robustness in the connected and unconnected case.

The second trophic level has the largest impact on the robustness increase. For small migration strengths, the robustness increase in the second trophic level is even larger than in the sum over all trophic levels as migration has a negative impact on the robustness of species of the third trophic level. This negative impact, however, decreases with increasing migration strength d and for large migration strengths, i.e. $d = 10^{-4}$, migration has no influence on the robustness of third trophic level species. Species of the first trophic level survive a little more often when species are able to migrate between patches and this positive effect increases slightly with increasing migration strength d. These effects happen a little less frequently when the migrating biomass B_{migr} increases and the migration strength d is high.

Species of the first trophic level rarely go extinct as they feed directly on the constant external resource. Consequently, they can rarely benefit from migration. This also explains the small error bars of the robustness increase in the first trophic level. Species of the second trophic level go extinct more frequently such that their benefit of migration is also much higher. They, however, survive with less biomass, since more species coexist. This leads to the robustness decrease in the third trophic level when migration strength is low. With increasing migration strength d, the number of species of the third trophic level that can survive due to migration increases and outweighs the robustness decrease caused by the lower consumption rates. Hence, species of the third trophic level can only benefit from migration when migration rates are high.

As there are much less species in higher trophic levels their impact on the robustness increase caused by migration is negligible.

4.6 Analysis of survival mechanisms

In this section, we identify the mechanisms that are responsible for the robustness increase that we have observed in Fig. 4.5. For deterministic migration, Plitzko and Drossel (2014) identified two mechanisms, namely:

1. The rescue effect: Species with unfavorable initial conditions on a patch can survive due to immigration from a neighboring patch where the species had more favorable initial conditions.

2. Dynamical coexistence: Species that can never coexist on unconnected patches can survive together due to the increased number of phase space dimensions which can increase the number of possible attractors.

More precisely, dynamical coexistence includes two types of species: (i) species that can never coexist locally, but that survive in part of the runs on different patches and (ii) species that can never survive on isolated patches as the species, with which they cannot coexist, survive independently of their initial conditions. We will focus here on the second case as in (Plitzko and Drossel, 2014), since this is a global effect and thus increases regional robustness. Furthermore, analyzing the first case would include much more computational effort.

In order to determine the impact of those two effects, we calculate population dynamics when the patches are unconnected and when migration is possible using the same initial conditions and the same food web in both cases. We then count the number of initial conditions under which each species survives considering 100 different initial conditions in total. Species that survive due to dynamical coexistence can *never* survive on unconnected patches, but do survive when being able to migrate. Species that can be rescued by immigration must survive in *part of* the runs. When this number increases when migration is switched on, species with unfavorable initial conditions are rescued from extinction due to immigration from neighboring patches. The resulting relative occurrence of dynamical coexistence and the rescue effect are averaged over 1000 different food webs. We consider four patches arranged in a chain for this investigation.

Fig. 4.7 shows the relative occurrence of dynamical coexistence (red) and the rescue effect (orange) in dependency of the migration strength d and for different migrating biomass units B_{migr}. For comparison, the results for deterministic migration are shown with dotted lines.

When the migration strength is low, species can only benefit from migration due to the rescue effect. This only occurs for stochastic migration as the incoming biomass is then larger than or equal to the extinction threshold[9] $B_{\text{exth}} = 10^{-5}$. Consequently, species can also be rescued in the adiabatic limit, but not when considering deterministic migration in the limit of small migration strength as the patches are then de facto unconnected. Species that can be rescued from extinction must survive on some patch where the species has more favorable initial conditions. Hence, the rescue effect increases local robustness, but not regional robustness, which means that the patches differ less when more species are rescued from extinction. This explains why the difference between local and regional robustness is lower for stochastic migration than in the deterministic limit (cp. Fig. 4.5). Dynamical coexistence cannot occur when the migration strength is low since the time between two migration events is too long to prevent the extinction of the species. As migration events only occur when population dynamics has reached an attractor, species cannot survive due to dynamical coexistence in the adiabatic limit.

The relative occurrence of both the rescue effect and dynamical coexistence increase with increasing migration strength d and are always higher or equal to those of the deterministic case in concert with local and regional robustness in Fig. 4.5. This is the case since the migrating biomass units are at least of the size of the extinction threshold $B_{\text{exth}} = 10^{-5}$ for stochastic migration in contrast to the deterministic limit.

The number of rescued species increases with the migration strength d since migration events happen more frequently. This also increases the probability that a migration event happens at a time at which the conditions for the rescue effect are convenient, for instance when a competing species has a small biomass. Similarly, the relative occurrence that a species is rescued due to migration decreases with increasing migrating biomass unit B_{migr}, since this includes a longer mean time between two migration events (s. Eq.(4.8)). With increasing migration strength d, the relative occurrence of the rescue effect for different migrating biomass units B_{migr} approach each other as the frequency of migration events increases with d (s. Eq.(4.8)). This also explains why we have observed that the difference of local and regional robustness decreases with increasing migration strength d and why this difference is higher for higher migrating biomass units B_{migr} (cp. Fig. 4.5).

[9] A rough estimate: As the mean biomass per species is approximately $\bar{B} = 1$ and the solver makes time steps of around $\Delta t = 0.01$, the biomass that migrates from one patch to a linked one in the deterministic limit is around $M(B_i) = 10^{-6}$ for $d = 10^{-4}$. Since species of the lower trophic levels regularly have a higher biomass, the probability to benefit from migration increases with decreasing trophic level.

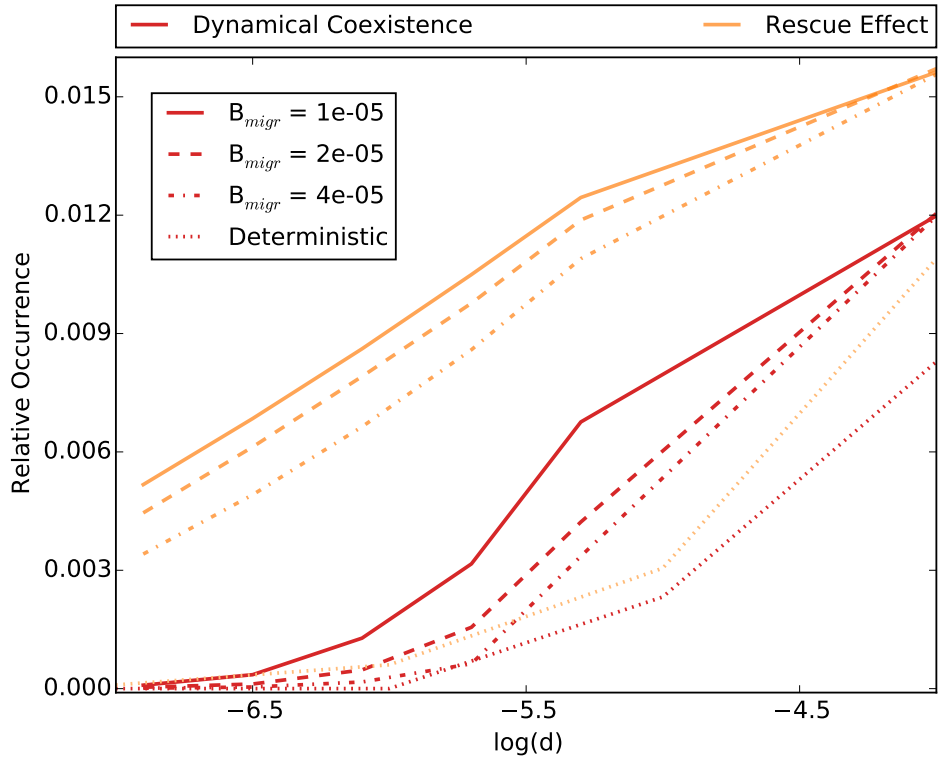

Figure 4.7.: Relative occurrences of dynamical coexistence (red) and the rescue effect (orange) in response to the migration strength d. The values were obtained by counting all cases where the corresponding effect occurred (over all species, initial conditions, and patches) and dividing it by the number of species, patches, and initial conditions.

Dynamical coexistence also becomes possible with increasing migration strength d as species can build up enough biomass to survive during periods of infrequent migration events. This is illustrated via an example time series of a species surviving due to dynamical coexistence in Fig. 4.8. As long as migration events happen frequently enough (i.e. when $B_{\text{migr}} = 10^{-5}$), the species can build up enough biomass to survive longer periods without any migration event. However, with increasing migrating biomass unit B_{migr}, migration events happen less frequently and the probability that the species does not survive at the end of the simulation increases. Consequently, the relative occurrence of dynamical coexistence decreases with increasing migrating biomass unit B_{migr} (s. Fig. 4.7).

The difference in the relative occurrence of dynamical coexistence between the migrating biomass units B_{migr} considered is largest for intermediate migration strength ($\log(d) \approx -5.3$) since migration events happen frequently enough to enable dynamical coexistence in this case, but the migration strength is low enough such that the migrating biomass unit B_{migr} has a crucial impact on the mean time between two migration events τ for enabling dynamical coexistence. As affecting species that cannot survive on unconnected or weakly connected patches, dynamical coexistence explains the increase in regional robustness with increasing d in Fig. 4.5.

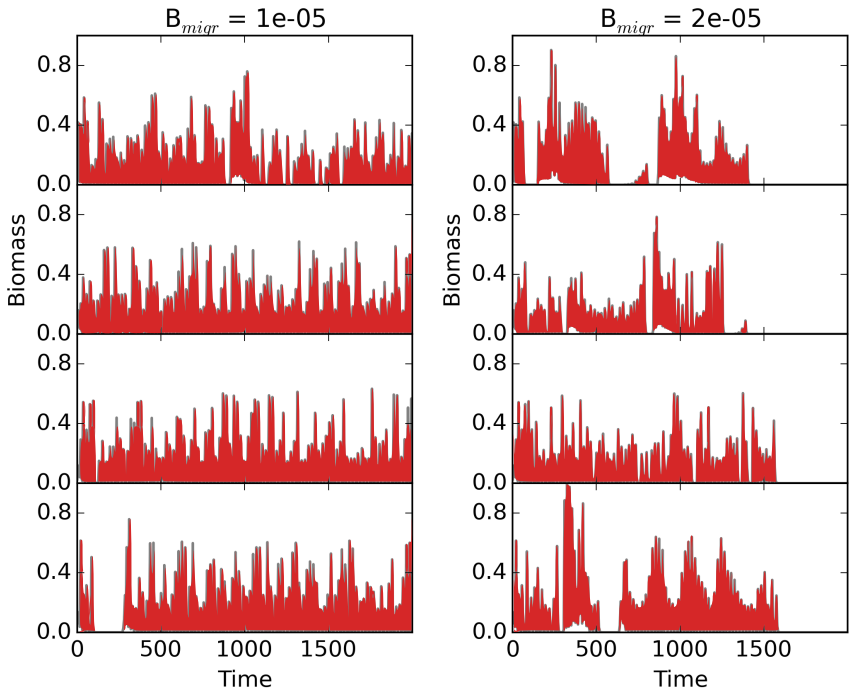

Figure 4.8.: Time series of a species surviving due to dynamical coexistence for $B_{\text{migr}} = 10^{-5}$ (left) and $B_{\text{migr}} = 2{\cdot}10^{-5}$ (right) on the four patches with a migration strength $d = 10^{-5.3}$.

4.7 Adiabatic limit

In this section, we focus on the adiabatic limit since this is the case where a deterministic modeling of migration is most inappropriate. As deduced in the previous section, species can only benefit from migration due to the rescue effect in this case. Under the assumption of a large spatial web, this may lead to three different spatial compositions in the long-term limit:

1. Each patch contains exactly the same food web.
2. The patches differ in the food web they contain, however, the composition is stationary.
3. There is ongoing species replacement, i.e. three (or more) species cyclically replace each other.

Here, we investigate which of these cases occur in our model. As we are interested in the long-term limit on a large spatial web, we use invasion experiments to find possible final states of the metacommunity in the adiabatic limit. In order to do this we categorize the species in three groups, namely, (i) species that *always* survive independently of their initial conditions (marked in white), (ii) species that survive in *part of* the runs as their survival depends on the initial conditions (marked in gray), and (iii) species that *never* survive independently of their initial conditions (marked in black). Only the species marked in gray that survive in *part of* the runs can be rescued due to migration. The procedure of the invasion experiments for one particular food web is then the following:

1. Identify all stable states the food web can be in when patches are unconnected.
2. Based on these stable states, classify the species in the three categories mentioned above.
3. Test for each stable state whether the immigration of all species that do not survive in this stable state, but that can survive in some stable state is successful one after the other. The invasion of a species can result in the extinction of other species. This either leads to a new or to a known stable state.
4. Repeat step 3 until no invasion is successful anymore.

We calculate population dynamics for 100 initial conditions per food web in order to identify all stable states and we use a migrating biomass unit of $B_{\text{migr}} = 10^{-5}$ for the invasion. We perform this investigation in three variants in order to get an impression of possible spatial compositions. First, we use food webs that contain 18 species including three basal ones as initial food web comparable to our investigation in Section 4.4; second, we consider a system that initially contains two different food webs each containing 6 species including one basal species. Finally, we construct food webs by hand taking the rules of the niche model into account in order to ensure that we have found examples for all possible spatial compositions.

4.7.1 Single initial food web

Let's focus on the variant where the system initially contains a single food web of 18 species. Fig. 4.9 shows an example which we explain in detail. On the top, the initial food web is shown and the species are marked according to their categories. After population dynamics the system can be in four stable states which are shown in the middle row of Fig. 4.9. Possible invaders are marked in gray.

Species 8 can only survive when species 1 survives as being its only prey. Species 13 and 16 can only survive when species 1 and consequently species 8 go extinct and vice versa. Hence, these species cannot coexist. Furthermore, species 2 must survive to enable the survival of species 13 and 16.

The invasion of species 2 is always successful, but can lead to the extinction of species 1 and 8. Species 1 can however reinvade again and thereafter the invasion of species 8 is also successful leading to the second stable state. Species 13 and 16, on the contrary, are not able to crowd species 1 (and species 8) out. Consequently, in the long-term limit all patches will contain the food web shown in the bottom row of Fig. 4.9 in the adiabatic limit. Hence, we found an example of the first spatial composition listed above, namely, that all patches contain the same food web in the long-term limit.

Indeed, we also found examples for the second spatial composition, namely a stationary one containing different food webs. An example is shown in Fig. 4.10. In this case, species 5 cannot coexist with species 2 and 9 whereas species 6 and 7 can coexist with all species, but not with each other as they have the same predators and prey and thus compete for the same niche (see middle row of Fig. 4.10). Indeed, the species cannot outcompete each other whereas species 2 and 9 crowd species 5 out. Consequently, the food webs in the long-term limit differ in whether containing species 6 or 7 as illustrated in the bottom row of Fig. 4.10. The species with the more favorable initial condition survives on a particular patch and cannot be crowded out. Hence, the two final food webs occur in similar frequency.

Both examples illustrate the rescue effect, as more species survive in the final food webs in the long-term limit as in the initial food webs, i.e. when the patches are unconnected. The example in Fig. 4.10 also explains the difference between local and regional robustness in the adiabatic limit in Fig. 4.5. For all analyzed examples, we verified our results by artificially removing parts of the species and testing the invasion of other species.

However, we could not find a food web that enables ongoing species replacement.

4.7.2 Two initial food webs

In a second step, we consider a system that initially contains two different food webs each containing 6 species including one basal species in order to test whether we observe ongoing species replacement in this case. We choose smaller food webs for this investigation to handle the complexity in a reasonable time. Invaders of the foreign food web can feed on all species that are in the feeding range of the considered species. Likewise, invaders are prey of all species, the feeding range of which encloses the niche value of the considered species.

Again, we found example systems that reach a stationary homogeneous and heterogeneous spatial composition in the long-term limit, whereby the final food web can contain only species of one food web or a new composition of species of both food webs. Hence, the two food webs can crowd each other out or can merge, whereby some species of each food web go extinct (s. Fig. 4.11 for an example). Again, more species survive in the final food web in the long-term limit than in the initial food webs after applying population dynamics illustrating the rescue effect in the adiabatic limit.

Again, we could not find an example system that shows ongoing species replacement.

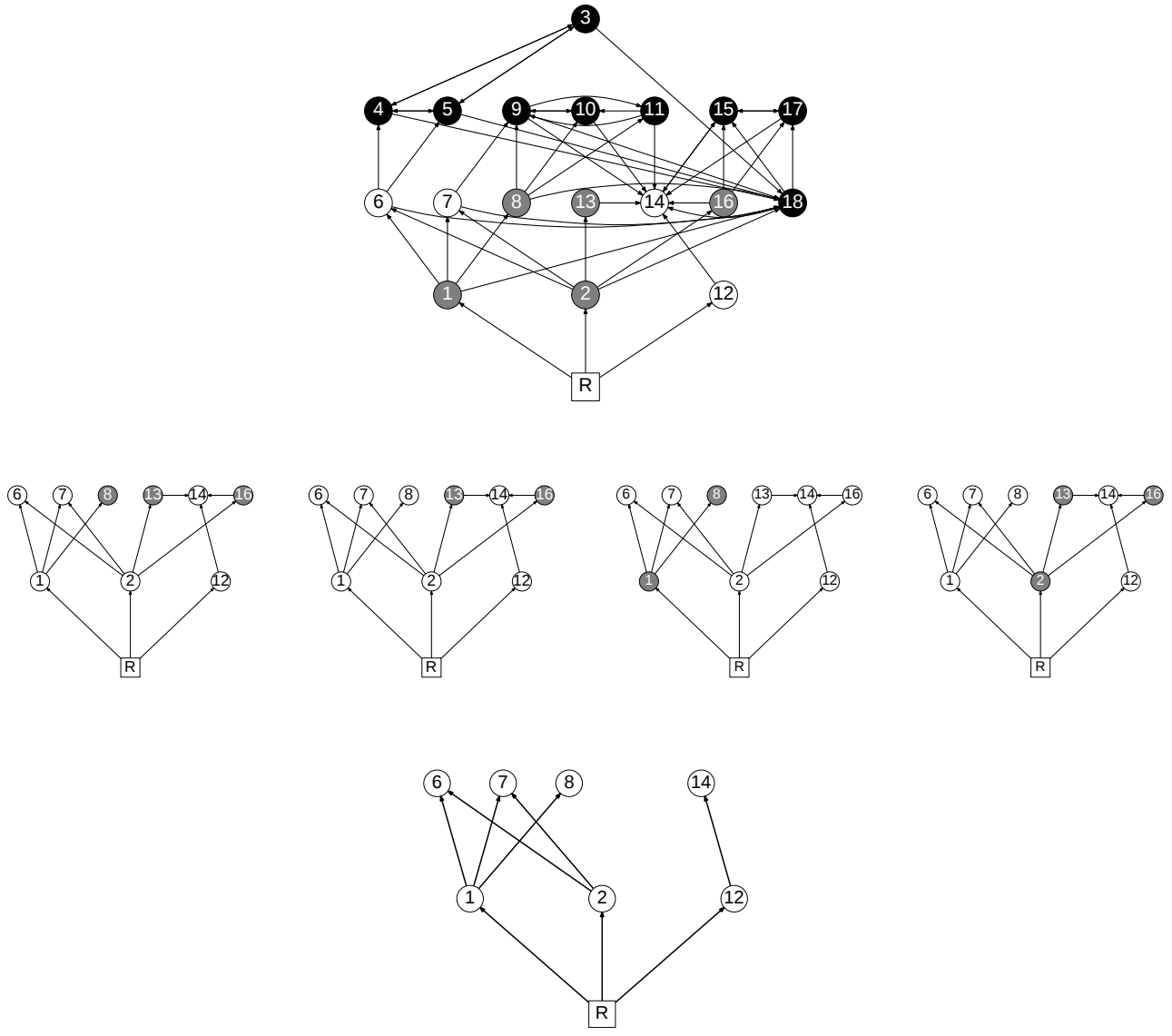

Figure 4.9.: Example food web at different points during the investigation. The node at the bottom represents the resource, and the vertical position indicates the trophic level of the species. First row: The initial food web. The colors indicate the fate of species after population dynamics. Black species always go extinct, while white species always survive. Species colored in gray survive dependent on the initial conditions. Second row: Possible networks resulting after population dynamics. The species colored in gray are possible invaders in the considered scenario while we colored those species that survive in this scenario also in white. Third row: Final food web being present on all patches in the adiabatic limit.

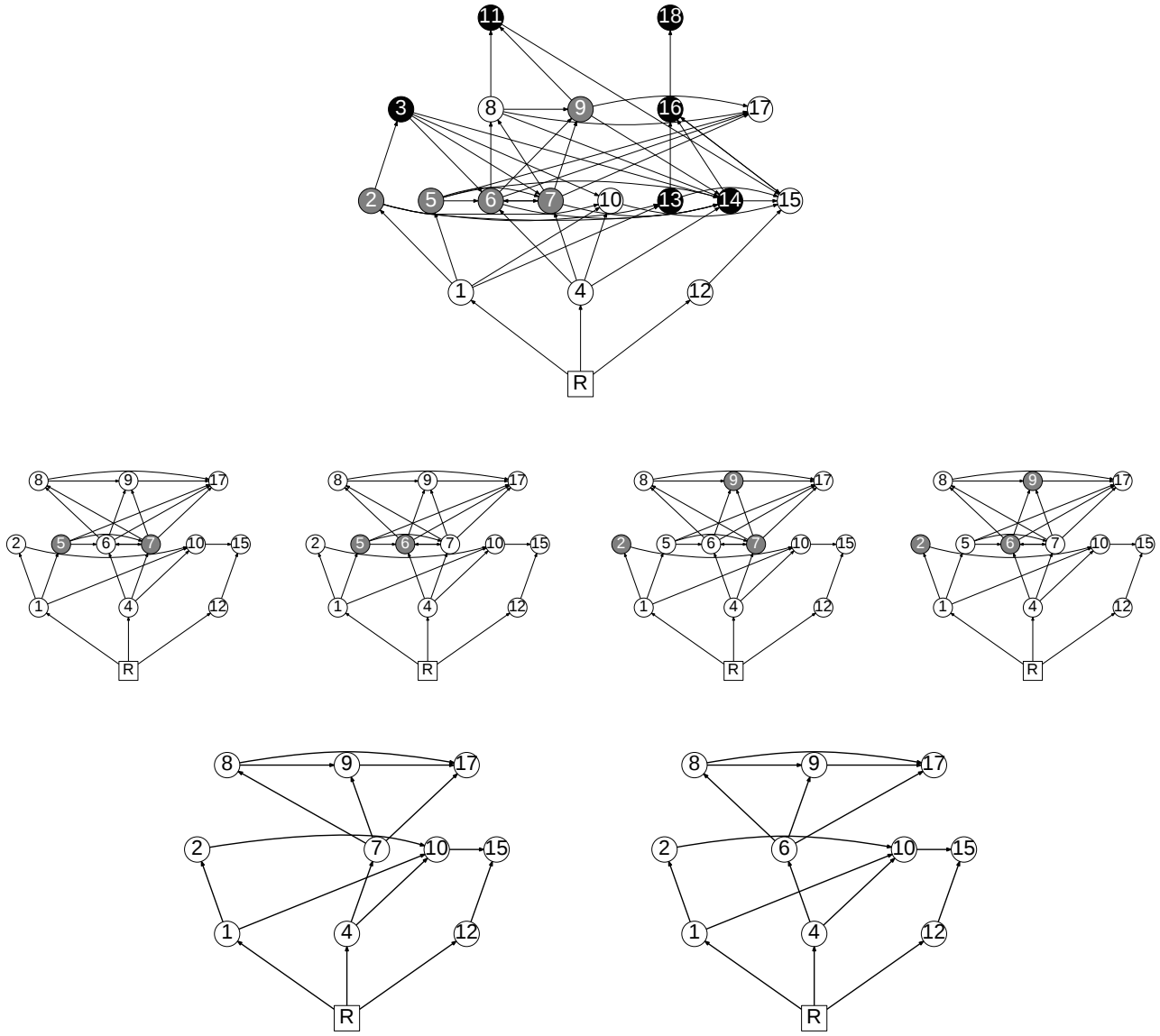

Figure 4.10.: Example food web at different points during the investigation. The node at the bottom represents the resource and the vertical position depicts the trophic level of the species. First row: The initial food web. The colors indicate the fate of species after running population dynamics. Black species always go extinct, while white species always survive. Species colored in gray survive dependent on the initial conditions. Second row: Possible networks after population dynamics. The species colored in gray are possible invaders in the considered scenario while we colored those species that survive in the considered scenario also in white. Third row: Food webs resulting in the adiabatic limit. In average the food web on the left hand side is present on 49% of the patches, the rest contains the food web on the right hand side.

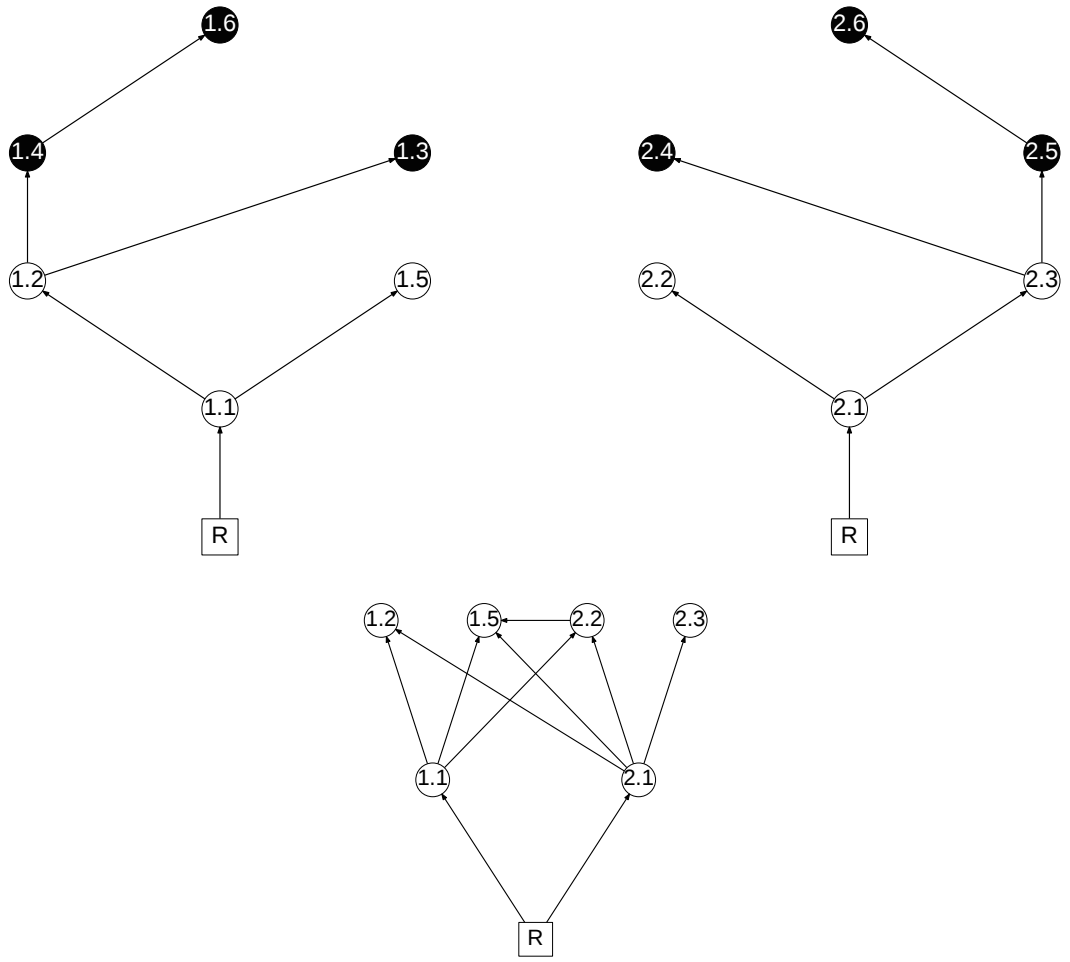

Figure 4.11.: Example of a system that contains initially two different food webs at different points during the investigation. The node at the bottom represents the resource and the vertical position depicts the trophic level of the species. First row: The two initial food webs. The colors indicate the fate of species after running population dynamics. Black species always go extinct, while white species always survive. In this case, there are no species that survive dependent on their initial conditions. Second row: The resulting food web in the adiabatic limit which contains species of both food webs.

4.7.3 Constructing food webs by hand

Finally, we construct food webs by hand, but in consideration of the rules of the niche model. Furthermore, we tune the parameters by hand and now assume that a species can attack its prey with different rates. Indeed, we can find ongoing species replacement in this case when considering the food web shown in the top row of Fig. 4.12. The feeding links that are depicted as dashed lines are much weaker than those marked as solid lines (by a factor 10^{-3}).

Since species 2, 3, and 4 are all prey and predator of each other and there is a considerable top down pressure due to species 5, they cannot coexist on an isolated patch leading to the possible networks after population dynamics, that are shown in the middle row of Fig. 4.12. When species 2 survives on a patch, it can be crowded out by species 3, which in turn can be replaced by species 4. Species 4, however, can be displaced by species 2 leading to an ongoing species replacement on a large spatial web in the long-term limit (see bottom row of Fig. 4.12).

We could thus find examples for all three spatial compositions defined above, although the patches only differ in the initial biomasses of species. Nevertheless, we conclude that although ongoing species replacement is possible, it happens very infrequently and is thus negligible in our model.

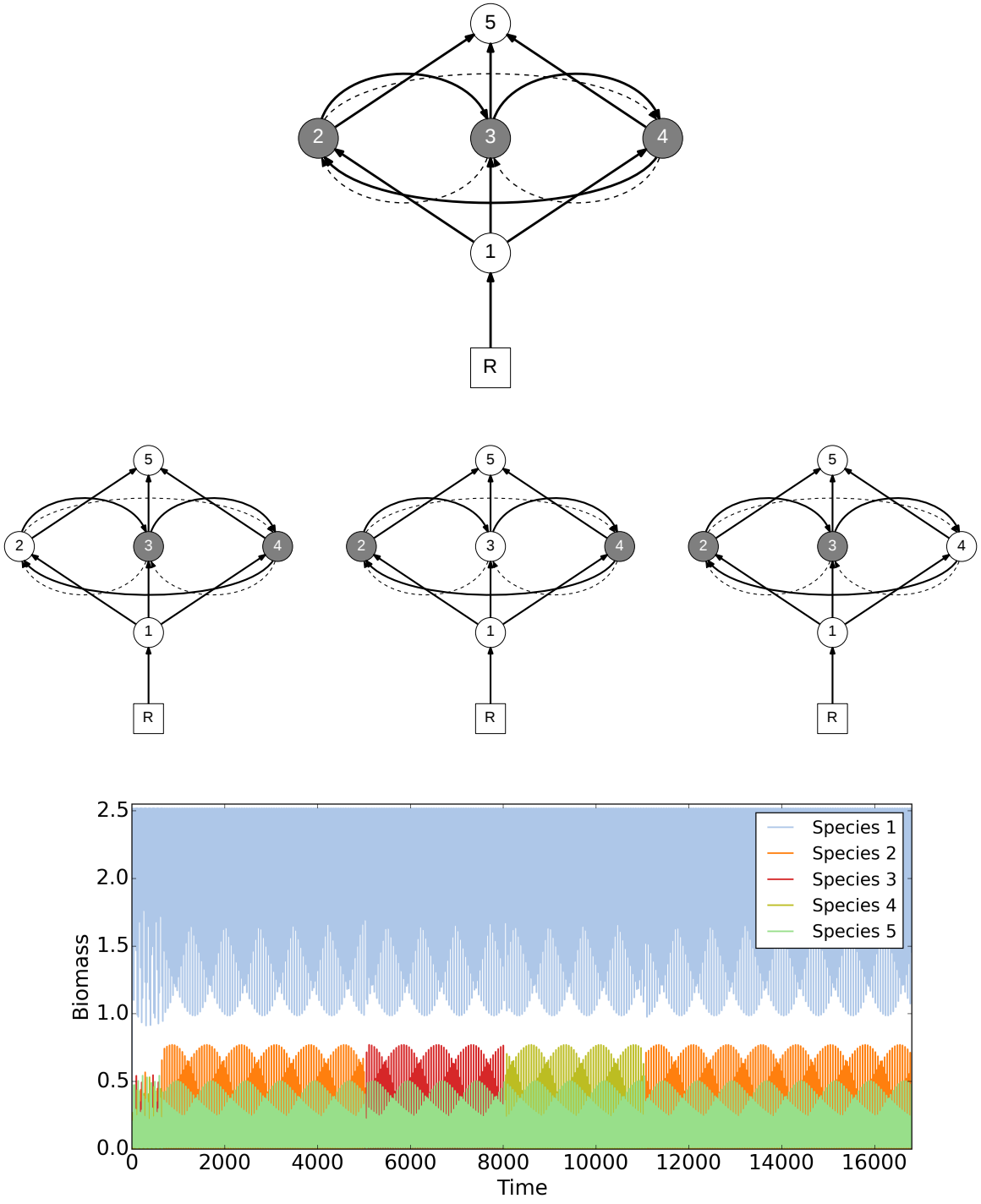

Figure 4.12.: Example food web that enables ongoing species replacement at different points during the investigation. The node at the bottom represents the resource and the vertical position depicts the trophic level of the species. First row: The initial food web. The colors indicate the fate of species after running population dynamics. White species always survive while species colored in gray survive dependent on the initial conditions. Second row: Possible networks after population dynamics. The species colored in gray are possible invaders in the considered scenario while we colored those species that survive in the considered scenario also in white. Third row: Time series of all species on one patch when species 3 immigrates at $t = 50052$, species 4 at $t = 80063$, and species 2 at $t = 110074$. We observe ongoing species replacement.

4.8 Impact of allometric scaling

It is widely accepted that food webs show a clear body-size structure (Brose et al., 2006a; Heckmann et al., 2012) which affects the biological rates of the species in the food web. This is called allometric scaling and is introduced in detail in Section 2.3. We did not implement allometric scaling to distill the effect of migration on food web stability and to compare our findings to the work of Plitzko and Drossel (2014). In order to convince ourselves that allometric scaling does not qualitatively change the results presented here, we investigate the impact of allometric scaling when four patches are arranged in a chain and stochastic migration is possible.

Empirically, predators are typically larger than their prey (about 0.5-4 orders of magnitude) (Brose et al., 2006a). We take this into account by defining the mass of species i as $m_i = 10^{x n_i}$ with the niche value n_i and the allometric scaling factor x. The mass of each species can now be used to scale the biological rates. By considering the scaling laws defined in Section 2.3 and by taking into account that the assimilation efficiency is (Heckmann et al., 2012)

$$\lambda_{ij} = \lambda \frac{m_j}{m_i}, \tag{4.10}$$

this changes the population dynamics in Eq.(4.5) to (Heckmann et al., 2012)

$$\begin{aligned} \frac{\mathrm{d}B_i^u(t)}{\mathrm{d}t} =& \lambda m_i^{-0.25} \sum_{j \in R_i} \frac{a f_i^u B_j^u}{1 + \sum_l a f_i^u h B_l^u} B_i^u \\ & - m_k^{-0.25} \sum_{k \in C_i} \frac{a f_k^u B_i^u}{1 + \sum_m a f_k^u h B_m^u} B_k^u \\ & - \alpha m_i^{-0.25} B_i^u - \beta m_i^{-0.25} \left(B_i^u\right)^2 + M_i^u\left(\vec{B}\right). \end{aligned} \tag{4.11}$$

We use Eq.(4.11) for the investigations in this section.

Fig. 4.13 shows the local (orange) and regional (red) robustness as a function of the logarithm of the migration strength d, assuming a migrating biomass unit of $B_{\mathrm{migr}} = 10^{-5}$. From top to bottom we increase the allometric scaling factors x, which means that the mass difference between predator and prey increases. For $x = 0$, all species have the same mass, for $x = 4$ predators are around ten times larger than their prey. This can easily be estimated since the difference between the niche value of a predator and a prey is around $n_{\mathrm{Pred}} - n_{\mathrm{Prey}} \approx 0.3$ and thus $\frac{m_{\mathrm{Pred}}}{n_{\mathrm{Prey}}} = 10^{x(n_{\mathrm{Pred}} - n_{\mathrm{Prey}})} \approx 10^{1.2}$ for $x = 4$.

In general, allometric scaling leads to higher robustness in concert to several other studies (Brose et al., 2006b; Heckmann et al., 2012). The increase of local and regional robustness with migration rate d is, therefore, smaller (local robustness increase: 0.026 without allometric scaling; 0.013 for $x = 2$; 0.006 for $x = 4$), but qualitatively the same trends are observable. We conclude that our results are still valid when taking allometric scaling into account.

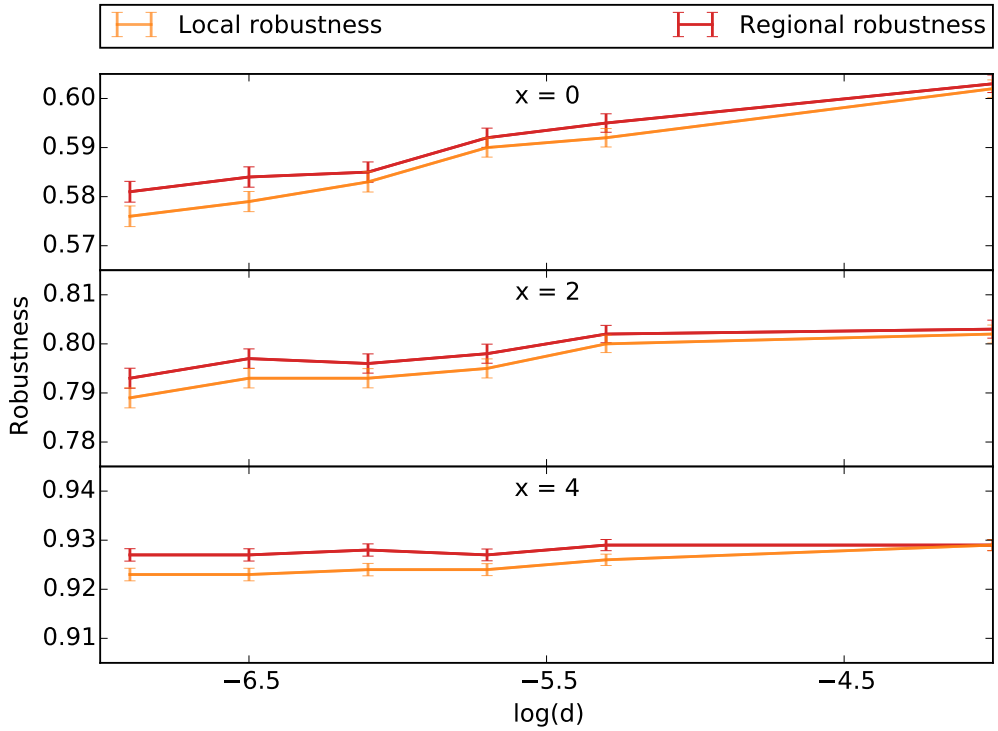

Figure 4.13.: Local robustness (orange) and regional robustness (red) as a function of the logarithm of the migration strength d, using different allometric scaling factors x and a migrating biomass unit of $B_{\text{migr}} = 10^{-5}$. The mass of each species is set to $m_i = 10^{x n_i}$, with n_i being the niche value of species i (Hamm and Drossel, 2017; Heckmann et al., 2012). For $x = 0$, all species have the same mass and allometric scaling is not considered, for $x = 4$ predators are around ten times larger than their prey.

4.9 Summary of major findings

Before discussing our results, we want to highlight some central findings with regard to our research questions (s. Section 4.3). We found that:

- Migration increases the local diversity even when migration rates are very small (adiabatic limit).
- In order to increase the diversity of the whole ecosystem (regional robustness), higher migration rates are necessary.
- The patch arrangement has no impact on local and regional robustness. However, the robustness increase is smaller for larger migrating biomass units B_{migr} and a smaller number of patches Y.
- Species of the second trophic level benefit the most from migration, even from small migration rates.
- Species of the third trophic level only benefit from migration when migration rates are large.
- In the adiabatic limit, a large spatial web can contain one static food web, different static food webs, or can show ongoing species replacement in the long-term limit. The latter is however negligible as occurring very infrequently.

4.10 Discussion

In this section, we investigated the impact of stochastic migration on a metacommunity in dependency of the migrating biomass unit, the number, and the arrangement of the patches. In order to do this, we constructed food

webs using the niche model which consists of 18 species. We placed the same food web on each patch, but with different initial biomasses of each species. Migration was modeled as a stochastic process with an emigration rate of each species that is proportional to its biomass density on the considered patch. When migration events are rare, this modeling approach provides more realistic results than a deterministic modeling as it takes into account that at least the biomass of one individual moves between the patches. For comparison, we also modeled the deterministic limit and the adiabatic limit, which means that migration events happen infrequently enough that the system reaches an attractor between two migration events.

We find that local and regional robustness[10] increase with increasing migration strength d and that local robustness is higher than on unconnected patches even in the limit of very small migration rates (i.e. in the adiabatic limit). Hence, migration increases local species diversity also in the limit of small migration rates. Indeed, empirical (Dey and Joshi, 2006; Molofsky and Ferdy, 2005; Holyoak and Lawler, 1996) and theoretical studies (Dey and Joshi, 2006; Molofsky and Ferdy, 2005; Plitzko and Drossel, 2014; Hauzy et al., 2010) also find that migration enhances the stability and diversity of food webs. However, these theoretical studies used a deterministic approach and thus found this enhancing effect only when migration rates are not too small, since patches are then effectively unconnected in the deterministic limit (Dey and Joshi, 2006; Molofsky and Ferdy, 2005; Plitzko and Drossel, 2014). Studies that showed this with a stochastic approach used simplified local food webs, as predator-prey systems (Yaari et al., 2012) or one trophic level (neutral model) (Economo and Keitt, 2008). Additionally, we find that the arrangement of the patches has no impact on the robustness. However, we show that robustness increases with the number of patches. Yaari et al. (2012) found similar results for a predator-prey system with stochastic migration and demographic stochasticity.

Furthermore, we find that the robustness increase due to migration is caused by two effects, namely, (i) the rescue effect and (ii) dynamical coexistence, for both a deterministic (Plitzko and Drossel, 2014) and a stochastic modeling of migration.

The rescue effect describes that species can survive despite of having unfavorable initial conditions on a patch due to immigration from neighboring patches (Plitzko and Drossel, 2014). This effect occurs more frequently with stochastic migration than in the deterministic limit and is even observable in the adiabatic limit. Consequently, local robustness/diversity increases due to migration, even if migration rates are very low.

Dynamical coexistence arises due to the increased phase space dimension which may result in additional attractors (Plitzko and Drossel, 2014). In this thesis, species that survive due to dynamical coexistence can never survive on isolated patches, since they cannot coexist with a well-established species. Dynamical coexistence thus increases regional robustness or diversity, but occurs only when the migration strength is not too low, because only then do migration events occur frequently enough to maintain species coexistence.

Furthermore, we find that the occurrence of both effects is higher than in the deterministic limit. Consequently, the same is true for species robustness. The reason is that the immigrating biomass is at least of the size of the extinction threshold and may thus have an impact on the ecosystem. Furthermore, the occurrence of both effects (and species robustness) increases with increasing migration strength d and decreasing migrating biomass B_{migr}. The reason is that the number of migration events increases and thus the probability that the events happen at an appropriate point in time.

Our results show that species of the second trophic level benefit the most from migration, even in the limit of very small migration rates. However, species of the third trophic level only profit from migration when migration rates are large. Species of the remaining trophic levels either only have small impact on species diversity or are little affected by migration. Higher trophic levels may have a larger impact when considering that the animal speed, and thus migration strength, also scales with the body mass of the species (Hirt et al., 2017).

In particular, we investigated the adiabatic limit on long time scales and on a large spatial web by performing invasion experiments in order to analyze which spatial compositions can be found in this limit. We find that a large spatial web can be homogeneous by ultimately containing only one food web or heterogeneous by containing two slightly different food webs. This occurs although the food webs initially only differ in the initial biomasses of the species. Hence, migration can act as a source of spatial heterogeneity even in the limit of very rare migration events. Furthermore, we could construct a system that shows ongoing species replacement. This effect is also known as ”rock-paper-scissors“ dynamic in literature (Kerr et al., 2006), where three different networks cyclically displace each other. However, ongoing species replacement happens very infrequently, such that it is negligible in our model. Ongoing species replacement may play a major role when considering a spontaneous extinction

[10] Robustness is the fraction of persisting species. For local robustness, we calculate the robustness of each patch and then average over all patches. For regional robustness, a species is count as a persisting one when it survives on any patch.

probability, as species densities often follow a limit cycle in our investigations and reach values near the extinction threshold.

In a nutshell, we showed that species diversity or robustness is higher when they can migrate than on isolated patches independent of the migration strength, but to increase regional diversity, the migration rate must not be too small. The major profiteer of migration are species of the second trophic level, while species of the third trophic level can only benefit from migration when migration rates are large.

5 Trait variability in a plant-herbivore system

In this chapter, we investigate the impact of plant trait variability on a plant-herbivore system. Not only plants, but species individuals in general typically differ in various traits as for instance in morphology[1] (Bolnick et al., 2002; Herrera, 2009), behavior (Bolnick et al., 2002; Tinker et al., 2008), and resource use (Herrera, 2009; Estes et al., 2003). This intraspecific trait variability emerges due to (i) genetic diversity (Albert et al., 2011, 2010; Hughes et al., 2008; Gibert and Brassil, 2014) and (ii) plastic response to natural conditions, also known as phenotypic plasticity (Albert et al., 2011, 2010; Whitham et al., 2003). "Phenotypic plasticity is the ability of an organism to change in response to stimuli or inputs from the environment" (Jorgensen and Fath, 2014). Intraspecific trait variability can be structured in three organization levels. These organization levels are (i) intra-population trait variability (populations of one species differ in their traits), (ii) inter-individual trait variability (individuals of one species differ in their traits), and (iii) intra-individual trait variability (traits vary within one individual of a species) (Albert et al., 2011, 2010; Bolnick et al., 2002). Although trait variability is observed in all three organization levels (Herrera, 2009; Siefert et al., 2015; Jung et al., 2010; Fridley and Grime, 2010) and several studies found evidence to suggest that intraspecific genetic diversity can have considerable influence on an ecosystem, for instance on population stability (Agashe, 2009) and species diversity (Booth and Grime, 2003; Hughes et al., 2008), the mechanisms behind these phenomena and the reasons why we observe such an enormous extent of trait variability are not well understood.

One hypothesis why intraspecific trait variability is such ubiquitous in many species is that it *per se* affects the consumer response to this species (Wetzel et al., 2016; Bolnick et al., 2011; Ruel and Ayres, 1999). This idea is based on a simple mathematical theorem which is called Jensen's inequality (Jensen, 1906) that is in principle applicable on all organization levels of trait variability named above. Jensen's inequality states that a concave upwards function (increasing slope; positive curvature) applied on the mean of a set of points is less or equal to the mean applied on the concave upwards function of these points (Jensen, 1906). The opposite is true when considering a concave downwards function (decreasing slope; negative curvature). Fig. 5.1 illustrates this effect. This means that two species populations that only differ in their trait variance, but have the same mean trait can experience different mean consumer responses.

Indeed, some studies have investigated the impact of trait variability on a consumer-resource system as we defined it in Eq.(2.1), assuming that the attack rate (via the foraging effort (Okuyama, 2008)) and the handling time is individual-dependent (Gibert and Brassil, 2014; Okuyama, 2008). For instance, they considered a trait that is Gaussian distributed (Gibert and Brassil, 2014). Both the attack rate and the handling time depend on this trait, such that the variance of the trait distribution determines the ranges in which the attack rate and handling time alter (Gibert and Brassil, 2014). Population dynamics then include the averaged consumption rate per predator (Gibert and Brassil, 2014; Okuyama, 2008). These studies found that increasing intraspecific trait variability can decrease the interaction strength and thus dampen the consumer-resource oscillation, whereby both predator and prey are less prone to extinction (Gibert and Brassil, 2014; Okuyama, 2008). Consequently, trait variability can increase species persistence (Gibert and Brassil, 2014; Okuyama, 2008).

In this chapter, we focus on a system of plants and insect herbivores, which cause the major feeding loss on plants (Schoonhoven et al., 2005). In plants, trait variability has an enormous extent (Herrera, 2009; Siefert et al., 2015) and even occurs on intra-individual scale, for instance, when the leaves of a plant individual differ in a trait (Herrera, 2009; Siefert et al., 2015). Such plant-herbivore interactions stand out from conventional consumer-resource interactions, for instance because the investigated main features, i.e. plant trait variability and herbivore preference, are usually not adapted on the typical time scale of feeding interactions. Hence, to appropriately investigate the impact of plant trait variability on our plant-herbivore system, the consumer-resource model as defined in Eq.(2.1) is not suitable.

Two plant traits that often considerably differ on intra- and inter-individual level are the nutrient and the defense level of the leaves/plants (Bryant and Kuropat, 1980; Siefert et al., 2015; Wetzel et al., 2016; Ruel and Ayres, 1999). For applying Jensen's inequality, we need to know how the herbivore response as a function of either of these plant traits behaves (cp. Fig. 5.1). Multiple studies investigated these dependencies, they, however, came to divergent results (Ruel and Ayres, 1999; Ayres et al., 1987; Clancy, 1992; Tao et al., 2014; Wetzel et al., 2016).

[1] This means the structure or form of the species (Begon et al., 1997).

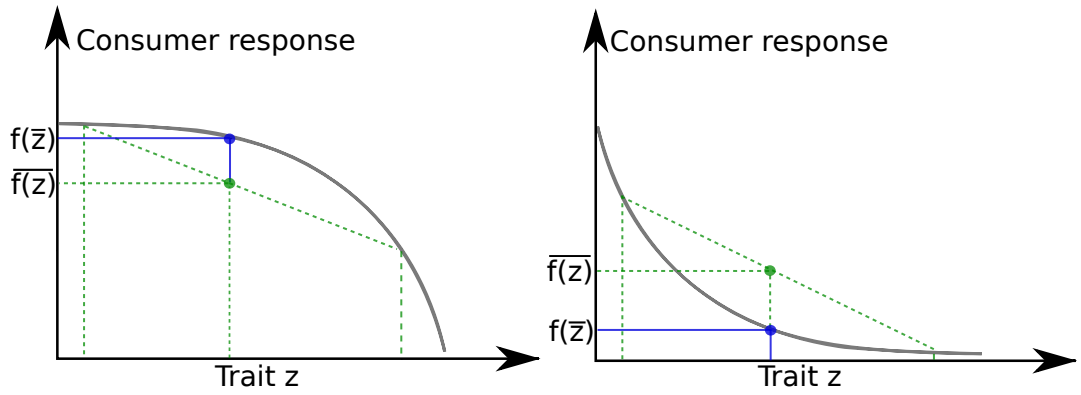

Figure 5.1.: Schematic illustration of Jensen's inequality. A consumer with a concave downwards response function of the variable trait z (left side of the figure) has a lower mean response when trait variability is large (i.e. $\overline{f(z)}$) than when just the mean trait has evolved (i.e. $f(\bar{z})$). The opposite is true when consumer response is a concave upwards function (right side of the figure).

In a meta-study, Wetzel et al. (2016) found that herbivore response is on average a concave downwards function of the plant nutrient level. This implies that the plant *per se* benefits from large nutrient level variability following Jensen's inequality as decreasing mean herbivore response (Wetzel et al., 2016) (cp. Fig. 5.1). Concerning the defense level of the leaves, Wetzel et al. (2016) found a linear herbivore response function, which implies that defense level variability has no impact in the plant according to Jensen's inequality.

However, herbivores have evolved different strategies to cope with plant defense. These strategies differ in the costs for dealing with plant defenses and thus in the herbivores' capability of feeding and growing on leaves with larger defense levels. Generalists use plants of several families as food source and only grow well on undefended and weakly defended leaves, while specialists focus on one plant family and can therefore deal well with the typical defenses of this plant family[2] (Lankau, 2007; Kliebenstein et al., 2002; Siemens and Mitchell-Olds, 1996; Poelman et al., 2008a). Furthermore, herbivores have evolved offensive traits that increase the benefits of feeding on the host plant (Karban and Agrawal, 2002). One example is that some specialists are able to convert the consumed plant defense into proper defense against predators leading to a reduction of predation risk (Dimarco et al., 2012; Rank, 1992; Despres et al., 2007; Karban and Agrawal, 2002). These sequestering specialists however also have to take higher energetic costs for dealing with plant defenses compared to the costs non-sequestering specialists have to take (Björkman and Larsson, 1991). Indeed, Ali and Agrawal (2012) suggest that the curvature of herbivore response as a function of the defense level differ with the different specialization strategies of herbivores although there are counterexamples (Wetzel et al., 2016). Consequently, herbivores with different specialization strategies may cause divergent *per se* effects of defense level variability on the plant.

Herbivores have evolved further strategies to react on environmental conditions (e.g. altering plant trait variability) including an adaptation of their behavior. For example, numerous studies found that herbivores have preference for leaves with certain traits (Via, 1986; Herrera, 2009; Tabashnik et al., 1981; Travers-Martin and Müller, 2008; Despres et al., 2007; Rausher, 1979) representing another example of herbivore offense (Karban and Agrawal, 2002). Herbivore preference can arise in form of (i) *oviposition* preference[3] (Via, 1986; Herrera, 2009; Tabashnik et al., 1981; Travers-Martin and Müller, 2008; Despres et al., 2007; Rausher, 1979) and (ii) *feeding* preference for leaves with certain traits (Mody et al., 2007; Lubchenco, 1978). Regularly, it is found that herbivores prefer leaves on which they or their offspring perform well (also known as "preference-performance hypothesis") (Soto et al., 2012; Tilmon, 2008; Gripenberg et al., 2010) although there are several counterexamples (Valladares and Lawton, 1991; Gripenberg et al., 2010; Hufnagel et al., 2017). These mismatches may for instance be based on temporal variations of the plant trait from oviposition to larval feeding (Björkman et al., 1997). Due to the numerous evidence for herbivore preference in nature and the fact that preference regularly increases the benefits of the herbivore feeding, it may also have a considerable impact on the *per se* impact of trait variability.

In this chapter, we investigate whether nutrient and/or defense level variability is *per se* beneficial for a plant and in particular, we analyze the impact of herbivore preference and different specialization degrees of the herbivore

[2] More precisely, specialists can be subdivided in oligophagous herbivores that feed on one plant family and monophagous herbivores that consume only a single plant species. The latter are very rare.

[3] This is egg laying preference.

on these results. In order to do this, we divide our investigation into two parts. First, we assume that plant leaves only differ in their nutrient concentration. Here, we investigate the impact of herbivore preference on the predictions of Jensen's inequality, i.e. whether a herbivore population benefits or suffers from large plant nutrient level variability dependent on the curvature of herbivore response function. We further identify several features that affect the extent of (optimal) herbivore preference. Optimal preference is the preference that maximizes herbivore population growth.

In the second part, we investigate the *per se* effect of defense level variability on a plant that is attacked by either generalists or sequestering or non-sequestering specialists. Again, we analyze the impact of herbivore preference and additionally, we take predation pressure on herbivores into account in order to ensure that sequestering specialists can make use of their ability to convert consumed plant defense. As young leaves often contain considerably higher defense and nutrient levels as old leaves (Gutbrodt et al., 2012; Marsh et al., 2018; Cao et al., 2018; Travers-Martin and Müller, 2008), we will in particular investigate the impact of this relationship between the nutrient and the defense level on our results. We thus investigate the *per se* effect of defense *and* nutrient level variability on the plant in this part.

The two parts base on papers that were created in collaboration with Sarah Gaschler, Karsten Mody, Nico Blüthgen, and Barbara Drossel. The first study is submitted with the title "Impact of herbivore preference on the benefit of plant trait variability" in "Theoretical Ecology" (Thiel et al., 2019a) and the second study with the title "Per se impact of plant defense level variability on specialist and generalist herbivores" in "Oikos" (Thiel et al., 2019b). Nico Blüthgen and Karsten Mody provided their expertise concerning biological questions and the relevance of this work for the ecological community. Additionally, they suggested helpful literature for comparison. Sarah Gaschler looked for appropriate parameter values in literature and contributed with helpful discussions about the model. Barbara Drossel gave general advice and had helpful ideas for the construction of the model. Furthermore, she had the idea of the much shorter analytical calculations shown in Section 5.4 than the previous version. Everything else, i.e. the basic construction of the model, the simulations, several robustness tests that are not all shown in this thesis, the interpretation of the results, and the draft of the paper manuscripts were done by the author of this thesis. Concerning the latter, Barbara Drossel, Nico Blüthgen, and Karsten Mody also provided linguistic revision.

In this chapter, we first introduce some basics and the basic model used in both studies. For each part, we then explain the specifications and the extensions to the model in the beginning of the corresponding section followed by the results and a discussion of the results. In the end of this chapter, we discuss the results in total.

5.1 Jensen's inequality

Jensen's inequality is a mathematical theorem that is based on non-linear averaging (Jensen, 1906). Considering a concave upwards[4] (i.e. positive curvature; increasing slope) function $f(z)$, it states that

$$f\left(\sum_i^n \lambda_i z_i\right) \leq \sum_i^n \lambda_i f\left(z_i\right), \tag{5.1}$$

with $\sum_i^n \lambda_i = 1$. For a concave downwards function the opposite is true, while the expressions are equal when $f(z)$ is linear. In Appendix F, we proof this theorem.

When we choose $\lambda_i = \frac{1}{n}$, this means

$$f(\bar{z}) = f\left(\frac{1}{n}\sum_i^n z_i\right) \begin{cases} \leq \sum_i^n \frac{1}{n} f\left(z_i\right) = \overline{f(z)} \text{ if } f \text{ concave upwards}, \\ = \sum_i^n \frac{1}{n} f\left(z_i\right) = \overline{f(z)} \text{ if } f \text{ linear}, \\ \geq \sum_i^n \frac{1}{n} f\left(z_i\right) = \overline{f(z)} \text{ if } f \text{ concave downwards}. \end{cases} \tag{5.2}$$

In Fig. 5.1 this statement is graphically illustrated. A continuous formulation is

$$f(\bar{z}) = f\left(\int z p(z) \mathrm{d}z\right) \begin{cases} \leq \int p(z) f(z) \mathrm{d}z = \overline{f(z)} \text{ if } f \text{ concave upwards}, \\ = \int p(z) f(z) \mathrm{d}z = \overline{f(z)} \text{ if } f \text{ linear}, \\ \geq \int p(z) f(z) \mathrm{d}z = \overline{f(z)} \text{ if } f \text{ concave downwards}. \end{cases} \tag{5.3}$$

[4] Another term for such a function is convex.

Biological systems are exposed to various biotic and abiotic conditions that differ in space and time and (maybe in response to this variation) individuals of species differ in their traits. Hence, Jensen's inequality (or Jensen's effect) is cited in multiple different ecological contexts. For example Jensen's inequality is applied in case of a nonlinear relationship between attack rates and body sizes (Bolnick et al., 2011). Furthermore, Jensen's inequality is used to explain why variance in temperature elevates metabolic rates of poikilotherms[5] (concave upwards function) (Ruel and Ayres, 1999), why variance in light regimes depresses primary production (i.e. the production of plant biomass (Begon et al., 1997)) (concave downwards function) (Ruel and Ayres, 1999), and why variance in tissue quality and secondary metabolites[6] in plants affects herbivore response (Ruel and Ayres, 1999).

In this chapter, we investigate the per se effect of nutrient and defense level variability in plants. In particular, we show the crucial impact of herbivore preference on these results.

5.2 Generation based modeling

In these studies, we describe population dynamics on generation basis, since the investigated main features, i.e. plant trait variability and herbivore preference, are usually not adapted on the typical time scale of feeding interactions. We rather assume that changes of these features are based on plastic responses to the environment or changes in the genotype. These features can hence be seen as evolutionary strategies. A typical quantity that is determined in such models is fitness. The mean population fitness $\overline{W}$ is defined as the mean number of offspring per individual that reach reproductive age. Hence, the population density $N(\tau)$ in generation τ is determined recursively by

$$N(\tau) = N(\tau - 1)\overline{W}\,. \tag{5.4}$$

This equation can also be derived from the basic consumer-resource model, i.e. Eq.(2.1), as shown in Appendix E. For this study, our model has other requirements, such that the model cannot be derived straightforwardly from the basic consumer-resource model. We value the per se effect of trait variability by calculating the mean herbivore fitness as it is a direct indicator for herbivore population growth and thus for the impact of the herbivore on the plant with proceeding time. We introduce our plant-herbivore model in detail in Section 5.3.

5.3 The model

In this section, we introduce the basic model that is used in both parts of this chapter. This model describes insect-herbivores feeding on a plant population whose leaves differ in a trait z. We specify the identity of this trait in each subsection individually. The specifications and additional features that are considered for each study are introduced in Section 5.4.1 and 5.5.1.

5.3.1 Plant trait distribution

We assume that the considered plant trait is Gaussian distributed, with a mean in the middle of the considered trait interval $z \in [0, z_{\max}]$, i.e. at $\bar{z} = z_{\max}/2$. The variance V_S of this distribution $p(z)$ determines the degree of heterogeneity of the leaves concerning the considered trait. The trait variance is a plant strategy (Wetzel et al., 2016; Bolnick et al., 2011) as it may depend on the surrounding conditions (e.g. herbivore preference) whether a broad or a narrow trait distribution is more favorable for the plant. We thus define the plant strategy parameter S as

$$S = \frac{1}{1 + V_S}\,, \tag{5.5}$$

such that $S \to 0$ represents a uniform distribution over the considered trait interval and $S \to 1$ a delta distribution, meaning that all leaves of all plant individuals have the trait $\bar{z} = z_{\max}/2$. In Fig. 5.2(a), the plant trait distribution is shown for different plant strategy parameter S.

[5] A poikilothermal organism "cannot regulate its body temperature except by behavioural means such as basking or burrowing" (Oxford University Press, 2019).

[6] Secondary metabolites are chemical substances that are generally attributed a defense function. It appears that they play no role in the pathways of the plant's normal biochemical synthesis (Begon et al., 1997).

5.3.2 Mean fitness

In order to value the *per se* effect of trait variability on the herbivore (i.e. of varying plant strategy parameter S), we use the mean fitness $\overline{W}_H$ of the herbivore population. As mentioned above, the mean fitness $\overline{W}_H$ describes the mean number of offspring per herbivore individual that reach reproductive age.

We denote the fitness of a herbivore individual that feeds on a leaf with trait z as $W_H(z)$. Furthermore, we call the distribution of herbivore individuals feeding on leaves with trait z, $\Phi(z)$. The mean fitness of the herbivore population is then

$$\overline{W}_H = \int_0^{z_{\max}} \mathrm{d}z\, \Phi(z) W(z)\,. \tag{5.6}$$

When the herbivores have no preference for leaves with certain traits, they are distributed on the leaves according to the plant trait distribution, i.e.

$$\Phi(z) = \frac{1}{\int_0^{z_{\max}} p(z)\mathrm{d}z} p(z) = \Gamma p(z)\,. \tag{5.7}$$

5.3.3 Fitness per trait

The fitness $W_H(z)$ of a herbivore individual feeding on a leaf with trait z depends on the growth of the herbivore on this leaf, which we will express in terms of a performance function $f(z)$. More precisely, we define the performance function $f(z)$ as the growth of a herbivore individual feeding on a leaf with trait z within the time from hatching to pupation[7]. We assume that the performance of a herbivore is proportional to its fitness. Hence, the fitness $W_H(z)$ of a herbivore individual feeding on a leaf with trait z can be expressed as

$$W_H(z) = \lambda_H f(z)\,, \tag{5.8}$$

with the number of offspring per unit growth that reach the reproductive age λ_H.

5.3.4 Preference function

We define the preference function $\Phi_p(z)$ as the probability that an adult herbivore lays eggs on a leaf with trait z. We model the preference via a Gaussian distribution with the mean at the maximum of the fitness $W_H(z)$ of the considered herbivore population. The variance V_p describes the extent of herbivore preference. For a better handling of the possible value range, we define the preference parameter as

$$\tau = \frac{1}{1+V_p}\,. \tag{5.9}$$

Hence, herbivores have no preference when $\tau \to 0$, and $\tau \to 1$ describes the unrealistic case that the preference function is a delta distribution which means that just those leaves are used for oviposition on which the herbivore population reaches its fitness maximum. In Fig. 5.2(b), the preference function is depicted for varying preference parameter τ when herbivores prefer leaves with maximal trait value. This is the case when the fitness $W_H(z)$ per trait is maximal at $z = z_{\max}$. Note that the preference function is a population average such that low herbivore preference may also represent divergent preference behavior of different herbivore individuals.

[7] This is based on holometabolous insects that experience the following life cycle: egg/embryo ⇒ larva ⇒ pupa ⇒ adult insect/ imago (Beutel et al., 2013; Wikipedians, 2011; Rivers, 2017). Our model, however, also applies for hemimetabolous insects that have no pupal stage, but show gradual change to the adult condition (Beutel et al., 2013). In this case, the performance function $f(z)$ is the growth of a herbivore individual feeding on a leaf with trait z within the time from hatching to sexual maturity.

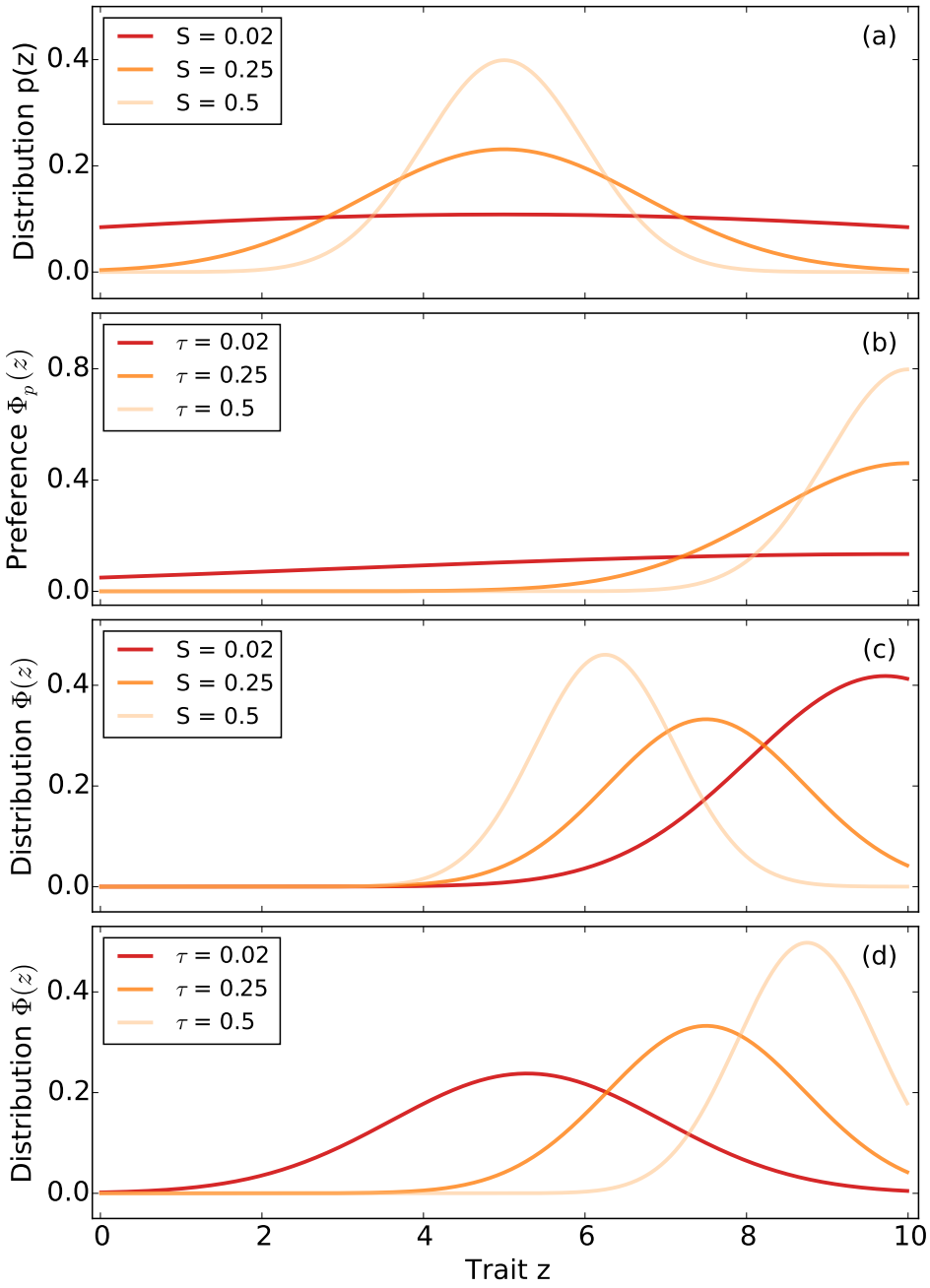

Figure 5.2.: (a) Trait distribution $p(z)$ for varying plant strategy parameter S (cp. Eq.(5.5)); (b) Preference function $\Phi_p(z)$ for varying preferences τ (cp. Eq.(5.9)) when the mean of the preference function is at $z = 10$, i.e. when high trait values are preferred; (c) Distribution $\Phi(z)$ of herbivores on leaves with trait z for varying plant strategy parameter S (cp. Eq.(5.5)) and a preference $\tau = 0.25$ (cp. Eq.(5.9)) when high trait values are preferred. These curves are the (normalized) product of the orange curve in (b) with the three curves in (a), respectively; (d) Distribution $\Phi(z)$ of herbivores on leaves with trait z for varying preferences τ (cp. Eq.(5.9)) and a plant strategy parameter $S = 0.25$ (cp. Eq.(5.5)) when high trait values are preferred. These curves are the (normalized) product of the orange curve in (a) with the three curves in (b), respectively.

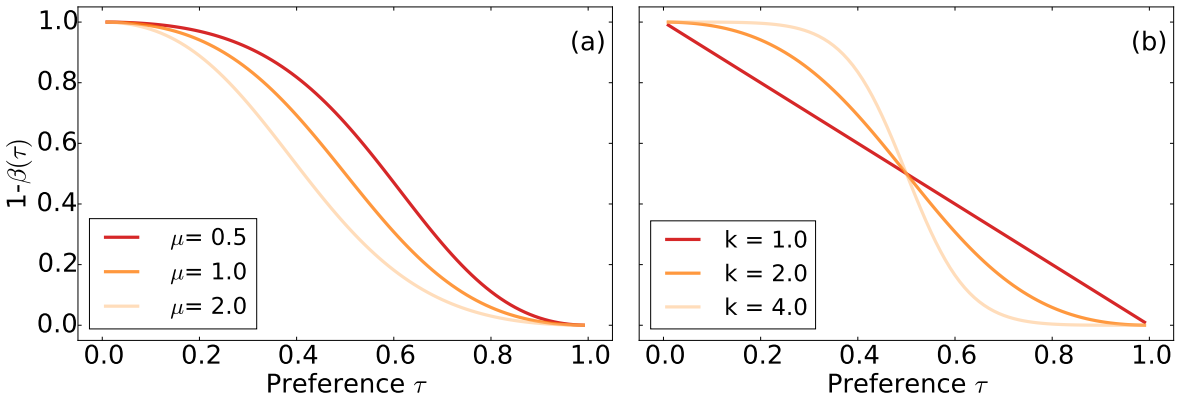

Figure 5.3.: Proportion of mass that remains considering preference, $1-\beta(\tau)$, for different values for the parameters (a) μ and (b) k that shape the the mass loss due to preference between the limits $\tau \to 0$ and $\tau \to 1$. We chose $k = 2$ in (a) and $\mu = 1$ in (b).

When herbivores show preference, the distribution $\Phi(z)$ of herbivore individuals on leaves with trait z additionally depends on the preference function $\Phi_p(z)$. Since we assume that the herbivore population is small enough to neglect intraspecific competition, the distribution $\Phi(z)$ of herbivore individuals on leaves with trait z is the normalized product of the trait distribution $p(z)$ and the preference function $\Phi_p(z)$, i.e.,

$$\begin{aligned}\Phi(z) &= \frac{1}{\int_0^{z_{\max}} \mathrm{d}z\, \Phi_p(z)p(z)} \Phi_p(z)p(z) \\ &= \Gamma \Phi_p(z)p(z)\,, \end{aligned} \tag{5.10}$$

with the normalization factor Γ.

Preferential behavior includes costs for finding appropriate leaves. We assume that these costs diminish herbivore growth. We thus consider a function representing the relative mass loss that interpolates between zero (when $\tau \to 0$) and one (when $\tau \to 1$) and whose exact form between these limits depends on parameters. A simple function that fulfills these requirements is

$$\beta = \frac{\mu}{\mu + (V_p)^k} = \frac{\mu \tau^k}{\mu \tau^k + (1-\tau)^k}\,, \tag{5.11}$$

where the parameters μ and k model the behavior of the mass loss due to preference between the limits $\tau \to 0$ and $\tau \to 1$. Fig. 5.3 shows the proportion of mass that remains considering preference, i.e. $1-\beta(\tau)$, for different values for the parameters μ and k. A larger μ includes higher costs for preference, while a larger k means that low preference includes lower costs, but high preference higher costs.

Incorporating the relative mass loss due to preference β in Eq.(5.6) for the mean fitness $\overline{W}_H$ of a herbivore population yields

$$\begin{aligned}\overline{W}_H &= (1-\beta) \int_0^{z_{\max}} \mathrm{d}z\, \Phi(z) W_H(z) \\ &\overset{(5.10)}{=} \Gamma(1-\beta) \int_0^{z_{\max}} \mathrm{d}z\, \Phi_p(z)p(z)W_H(z) \\ &\overset{(5.8)}{=} \Gamma \lambda_H (1-\beta) \int_0^{z_{\max}} \mathrm{d}z\, \Phi_p(z)p(z)f(z)\,, \end{aligned} \tag{5.12}$$

where Γ normalizes the distribution $\Phi(z)$ of herbivore individuals on leaves with trait z to one. This is the basic model, we will use in the following investigations.

5.4 Impact of herbivore preference on the benefit of plant nutrient level variability

In this section, we investigate the *per se* impact of plant nutrient level variability on herbivore fitness in dependency of the curvature of the herbivore performance function. In particular, and in contrast to previous studies (Wetzel et al., 2016; Ruel and Ayres, 1999), we are interested in the impact of herbivore preference on these findings, since herbivore preference is a phenomenon regularly found in nature (Via, 1986; Herrera, 2009; Tabashnik et al., 1981; Travers-Martin and Müller, 2008; Despres et al., 2007; Rausher, 1979).

In order to distill the effect of plant nutrient level variability, we neglect correlated changes in the secondary metabolites (i.e. in defense) and the impact of higher trophic levels in this section. For the same reason, we assume that the plant population is constant over the time interval covered in our model. This is a valid assumption when the plant population is large compared to the herbivore population and thus changes little due to herbivory. In Section 5.5, we investigate the impact of a positive correlation between the nutrient and the defense level in a leaf and in Appendix H, we consider that the plant population changes with time and analyze conditions that enable coexistence.

5.4.1 Specification of the model

In this section, we consider the nutrient level n of the leaves as variable trait. We evaluate herbivore fitness as described in Eq.(5.12). However, we still need to specify the performance function used in this study and the values of the parameters defined in the general model in Section 5.3.

Performance function

We use three different performance functions $f(n)$ qualitatively differing in their curvature, i.e. a concave upwards (increasing slope; positive curvature), a linear, and a concave downwards (decreasing slope; negative curvature) function. Furthermore, we consider monotonically increasing functions which are for instance suitable when the nutrient level describes the food quality from the herbivores' point of view. They are shown in Fig. 5.4. With this approach, we can distill the impact of the curvature of the performance functions on herbivore fitness. We choose the performance functions such that they have the same mean performance in order to ensure that the resulting mean fitness values are in the same order of magnitude (Thiel et al., 2019a). Note, that the fitness $W_H(n)$ of a herbivore individual feeding on a leaf with nutrient level n only differs by a constant factor from the performance function $f(n)$ (s. Eq.(5.8)). The maximum of the performance function $f(n)$ thus coincides with the maximum of the fitness $W_H(n)$ of a herbivore individual feeding on a leaf with nutrient level n. Consequently, the maximum of the herbivore preference function $\Phi_P(n)$ is at $n = n_{\max}$.

Each performance function is reasonable considering different nutrients or nutrient level ranges: When the nutrient typically limits the growth of the herbivore in the considered nutrient level range, a concave upwards performance function is appropriate. However, when herbivore growth is additionally dampened, for instance by a conversion process that requires energy, a linear performance function is suitable. A concave downwards performance function applies when the considered nutrient does not limit growth or when we consider a nutrient in a concentration range such that overall limits of herbivore growth become visible.

Empirical studies often find s-shaped functions, having both concave upwards and downwards regions, for the dependency of herbivore performance on leaves with nutrient level n (Clancy, 1992). However, we are interested in the impact of the curvature of the herbivore performance function on herbivore fitness based on Jensen's inequality (s. Section 5.1) and we thus do not consider s-shaped performance functions. The result for a s-shaped performance function can be estimated from this study by appropriately averaging the results for a concave up- and downwards performance function.

Regularly, performance functions having an optimum at intermediate nutrient levels are found in empirical studies considering nitrogen (Zehnder and Hunter, 2009; Joern and Behmer, 1998; Fischer and Fiedler, 2000; Joern and Behmer, 1997) or phosphorus (Boersma and Elser, 2006) as nutrient. More precisely, these studies found performance functions that have a form like a concave downwards parabola. This is the case when the nutrient level does not describe the food quality from the herbivores' point of view such that excess nutrients include costs because

- the nutrient level is correlated with another trait as the secondary metabolites in a leaf (Tao et al., 2014), or

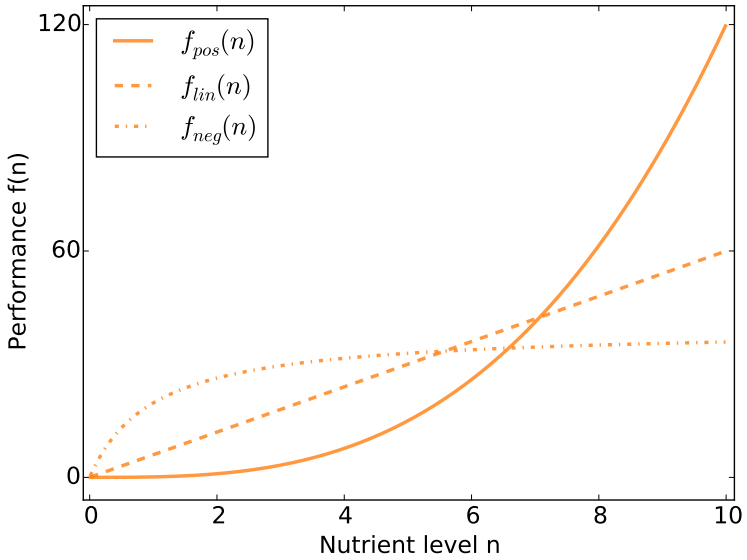

Figure 5.4.: The three types of herbivore performance functions considered in our study: $f_{\text{pos}}(n) = 0.12n^3$, $f_{\text{lin}}(n) = 6n$, $f_{\text{neg}}(n) = \frac{300}{10-\ln(11)}\frac{n}{n+1}$.

- the removal of excess nutrients includes metabolic costs (Tao et al., 2014).

Consequently, we also test the validity of our results under the assumption of this kind of performance function.

Choice of parameter values

We suppose that the nutrient level varies in $n \in [0, 10]$. By choosing appropriate units for the nutrient level each interval can be mapped onto this one. For the parameters that model the costs for preference (cp. Eq.(5.11)), we choose $\mu = 1$ and $k = 2$, such that is worth to show preference, but strong preference includes considerable losses (s. Fig. 5.3). For the remaining parameters, we pick the forest tent caterpillar (*Malacosoma disstria*) as model species[8]. *Malacosoma disstria* has a typical mass gain until pupation of 300 mg and produces around 300 eggs with a survival rate of 1/100 resulting in a number of offspring reaching reproductive age per unit of growth of $\lambda_H = 0.01\,\frac{1}{\text{mg}}$ (Hemming and Lindroth, 1999). We further normalize the performance functions to 300 mg, i.e. $\int \mathrm{d}n f(n) = 300$. Note that the parameter values only have a quantitative impact on the results.

Useful integral

In this section, we have to solve integrals of the form

$$\Gamma \int_{-\tilde{x}}^{\tilde{x}} C x^t e^{-bx^2}\,\mathrm{d}x\,, \tag{5.13}$$

several times with $t \in \mathbb{N}$ and

$$\frac{1}{\Gamma} = \int_{-\tilde{x}}^{\tilde{x}} e^{-bx^2}\,\mathrm{d}x\,. \tag{5.14}$$

Indeed, this integral can generally be solved resulting in

[8] Note, that these parameters are scaled allometrically as they are based on measured values.

$$
\begin{aligned}
&\Gamma \int_{-\tilde{x}}^{\tilde{x}} C x^t e^{-bx^2}\,\mathrm{d}x \\
&= \begin{cases} 0 \text{ if t odd, or} \\ \frac{C\prod_{i=1}^{t/2}(2i-1)}{(2b)^{t/2}} - \frac{\Gamma C}{b}\left(\sum_{i=0}^{t/2} \frac{\prod_{j=1}^{t/2}(2j-1)}{(2b)^{t/2-i}} \tilde{x}^{2i-1} e^{-b\tilde{x}^2}\right) \text{ if t even.} \end{cases}
\end{aligned} \tag{5.15}
$$

If t is odd, the integral is zero because of the symmetry of the integrand with respect to $x = 0$. For an even t, the result is obtained by applying integration by parts $\frac{t}{2}$ times as

$$
\begin{aligned}
\Gamma \int_{-\tilde{x}}^{\tilde{x}} C x^t e^{-bx^2}\,\mathrm{d}x &= \Gamma \int_{-\tilde{x}}^{\tilde{x}} C x^{t-1} x e^{-bx^2}\,\mathrm{d}x \\
&= \left[-\frac{\Gamma C}{2b} x^{t-1} e^{-bx^2}\right]_{-\tilde{x}}^{\tilde{x}} + \Gamma \int_{-\tilde{x}}^{\tilde{x}} \frac{C(t-1)}{2b} x^{t-2} e^{-bx^2}\,\mathrm{d}x\,.
\end{aligned} \tag{5.16}
$$

5.4.2 Research questions

We divide our investigation into two parts. First, we consider that herbivores have no preference, i.e. $\tau = 0$ (cp. Eq.(5.9)). Here, we investigate:

- Under which conditions is nutrient level variability *per se* beneficial for the plant?

In the second part, we focus on the impact of herbivore preference (i.e. $\tau > 0$) on these results. Hence, we tackle the following questions:

- What impact has herbivore preference on the *per se* effect of nutrient level variability?
- Which quantities influence the extent of herbivore preference?

In the following, we present our results concerning these research questions.

5.4.3 Herbivore fitness in response to plant nutrient level variability without herbivore preference

First, we assume that herbivores show no preference, i.e. $\tau = 0$ and thus suffer no loss due to preference, i.e. $\beta = 0$. In this case, the preference function is a uniform distribution, such that the distribution $\Phi(n)$ of herbivores on leaves with nutrient level n only depends on the nutrient distribution $p(n)$ as in Eq.(5.7). The mean fitness of the herbivore population defined in Eq.(5.12) thus simplifies to

$$
\overline{W}_H = \Gamma \lambda_H \int_0^{n_{\max}} \mathrm{d}n\, p(n) f(n)\,. \tag{5.17}
$$

Fig. 5.5 shows the mean herbivore fitness in dependency of the plant strategy parameter S (i.e. the extent of plant nutrient level variability; cp. Eq.(5.5)) under the assumption of (a) the concave upwards, (b) the linear, and (c) the concave downwards performance function shown in Fig. 5.4.

As predicted by Jensen's inequality (s. Section 5.1), a herbivore having a concave upwards performance function benefits from large nutrient level variability (i.e. small S) (cp. Fig. 5.5(a)), while herbivore fitness does not change as a function of the plant strategy parameter S when the performance function is linear (cp. Fig. 5.5(b)). The fitness of herbivores having a concave downwards performance function increases with the plant strategy parameter S, i.e. with decreasing nutrient level variability (cp. Fig. 5.5(c)). Hence, the plant benefits from large nutrient level variability when the herbivore performance function is concave downwards.

Indeed, Jensen's inequality can be applied on our model using the form in Eq.(5.3). We find that

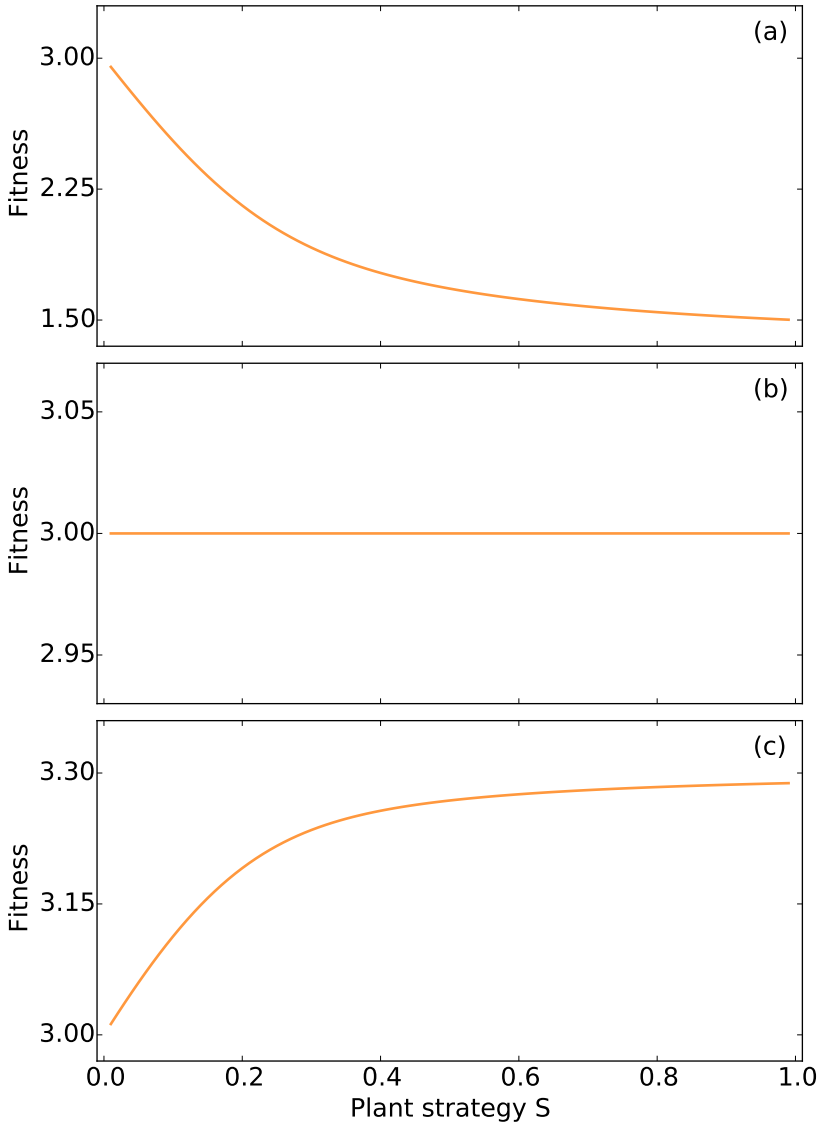

Figure 5.5.: Fitness of a herbivore population (i.e. mean number of offspring per herbivore individual reaching reproductive age; cp. Eq.(5.17)) in response to the plant strategy parameter S (cp. Eq.(5.5)) using (a) the concave upwards, (b) the linear, and (c) the concave downwards performance function shown in Fig. 5.4.

$$\int p(n)f(n)\,\mathrm{d}n \gtreqless \int \delta(n-\bar{n})f(n)\,\mathrm{d}n = f(\bar{n})\,, \tag{5.18}$$

under the assumption that $f(n)$ is a concave upwards ($\geq$), linear ($=$), and a concave downwards ($\leq$) performance function and that the nutrient distribution $p(n)$ has a non-zero width, i.e. $S < 1$. The difference between the two sides of the inequality increases with decreasing plant strategy parameter S (s. Fig. 5.5). Hence, we can deduce that

$$\int p(n,S_1)f(n)\,\mathrm{d}n \gtreqless \int p(n,S_2)f(n)\,\mathrm{d}n\,, \tag{5.19}$$

depending on the curvature of the performance function as defined above when $S_1 < S_2$.

Additionally, this result can be shown via an analytical calculation of the mean fitness (cp. Eq.(5.17)) as a function of the plant strategy parameter S (cp. Eq.(5.5)) that is Taylor expanded for small variations of the nutrient level n around the mean nutrient level $\bar{n}$. This calculation will act as a basis for the following part, where we take herbivore preference into account. In order to achieve this, we approximate the performance functions by a polynomial in n, the curvature of which depends on a parameter c. i.e.

$$f(n) = hn + cn^2\,, \tag{5.20}$$

with the curvature parameter c. The performance function is concave upwards when $c > 0$, linear when $c = 0$, and concave downwards when $c < 0$. Hence, by choosing $h = 6$ and $c = 0$, we receive the linear performance function f_{lin} in Fig. 5.4. The performance functions f_{pos} and f_{neg} (cp. Fig. 5.4) can also be transformed to the performance function defined above with $c > 0$ and $c < 0$, respectively, by using a Taylor expansion around the mean nutrient level $\bar{n}$, appropriately choosing the parameter h, and neglecting constant terms since they have no qualitative impact on the fitness landscape (cp. Eq.(5.15)).

For this calculation, we assume $h \geq 0$ in order to ensure that the performance can be positive for $n \geq 0$ and $c < 0$. We start with Eq.(5.17), i.e.

$$\overline{W}_H = \lambda_H \Gamma \int_0^{n_{\max}} \mathrm{d}n\, e^{-\frac{(n-\bar{n})^2}{2V_S}} \left(hn + cn^2\right) \tag{5.21}$$

and substitute $b = \frac{1}{2V_S}$ as well as $x = n - \bar{n} = n - \frac{1}{2}n_{\max}$ leading to

$$\begin{aligned}\overline{W}_H &= \lambda_H \Gamma \int_{-\tilde{x}}^{\tilde{x}} \mathrm{d}x\, e^{-bx^2} \left(h(x+\bar{n}) + c(x+\bar{n})^2\right) \\ &= \lambda_H \Gamma \int_{-\tilde{x}}^{\tilde{x}} \mathrm{d}x\, e^{-bx^2} \left(h\bar{n} + c\bar{n}^2 + x(h+2c\bar{n}) + cx^2\right).\end{aligned} \tag{5.22}$$

In Eq.(5.15), we formulated a general expression to solve such kind of integral. By applying this expression, we find

$$\overline{W}_H = \lambda_H \left(\underbrace{h\bar{n} + c\bar{n}^2}_{W_0} + \frac{c}{2b}\left(1 - 2\Gamma\tilde{x}e^{-b\tilde{x}^2}\right)\right). \tag{5.23}$$

Hence, for small variations around the mean nutrient level, i.e. around $\tilde{x} = 0$, we find with $b = \frac{1}{2V_S} = \frac{S}{2(1-S)}$ (cp. Eq.(5.5)),

$$\begin{aligned}\overline{W}_H &= \lambda_H\left(W_0 + \frac{c}{2b}\right)\\ &= \lambda_H\left(W_0 + \frac{c(1-S)}{S}\right).\end{aligned} \tag{5.24}$$

This confirms our previous findings (cp. Fig. 5.5); it shows that the mean fitness increases with increasing plant nutrient level variability, i.e. with decreasing S or b, when $c > 0$, which means that the performance function is concave upwards. When considering a concave downwards performance function (i.e. $c < 0$), mean fitness decreases with decreasing S or b which means that herbivores suffer from large nutrient level variability. Under the assumption of a linear performance function (i.e. $c = 0$) mean fitness does not depend on the plant strategy parameter S.

The only assumptions that we used for this calculation are:

- The performance function is (approximately) described by Eq.(5.20).
- The parameters h and c are chosen such that the performance function is larger or equal to zero around the mean nutrient level.

Hence, the result of our calculation also applies for a concave downwards parabola as performance function[9] as often found in empirical studies (Zehnder and Hunter, 2009; Joern and Behmer, 1998; Fischer and Fiedler, 2000; Joern and Behmer, 1997; Boersma and Elser, 2006).

5.4.4 Herbivore fitness in response to plant nutrient level variability and herbivore preference

In this section, we investigate the impact of herbivore preference ($\tau > 0$) on the results of the previous section. Fig. 5.6 depicts the mean fitness of a herbivore population as defined in Eq.(5.12) in color code when the herbivore population has the (a) concave upwards, (b) linear, and (c) concave downwards performance function shown in Fig. 5.4 in response to herbivore preference τ (cp. Eq.(5.9)) and the plant strategy parameter S (cp. Eq.(5.5)).

The fitness changes most with plant strategy parameter S when S is small since Jensen's effect is strongest in this case (cp. Fig. 5.1). For the same reason the fitness varies less with S for the concave downwards than the concave upwards performance function as the former changes less in the relevant range (i.e. around $n \geq \bar{n} = 5$; cp. Fig. 5.4).

Furthermore, herbivore preference can considerably alter the findings of the previous section, i.e. that the curvature of the herbivore performance function determines whether the herbivore benefits or suffers from large nutrient level variability. When the herbivore population has a concave upwards performance function, the herbivore benefits from large nutrient level variability (i.e. small S) independently of its preference τ as illustrated by the color change from lighter to darker color with decreasing S. This is in concert with our findings of the previous section (cp. Fig. 5.6(a) and 5.5(a)). However, under the assumption of a linear or a concave downwards performance function, the herbivore also benefits from large nutrient level variability (i.e. small S) when having considerable preference (cp. Fig. 5.6(b), (c)). More precisely, this is the case when $\tau > 0$ for the linear and approximately $\tau > 0.05$ for the concave downwards performance function. When the herbivores show less preference, the mean fitness decreases with decreasing plant strategy parameter S (cp. Fig. 5.6(c) and 5.5(c)).

Analytic calculation with preference

In order to understand this result more deeply and to show that it is generic, we again reconstruct this result analytically. By using the performance function $f(n) = hn + cn^2$ of the previous section, we calculate the mean fitness $\overline{W}_H$ (cp. Eq.(5.12)) near the mean nutrient level $\bar{n}$. In this case, the preference function $\Phi_p(n)$ can be Taylor expanded, and for small preferences τ, we find

$$\Phi_p(n) = \alpha(\tau n + 1), \tag{5.25}$$

[9] An example would be $f(n) = 10n - n^2$, i.e. $h = 10$ and $c = -1$.

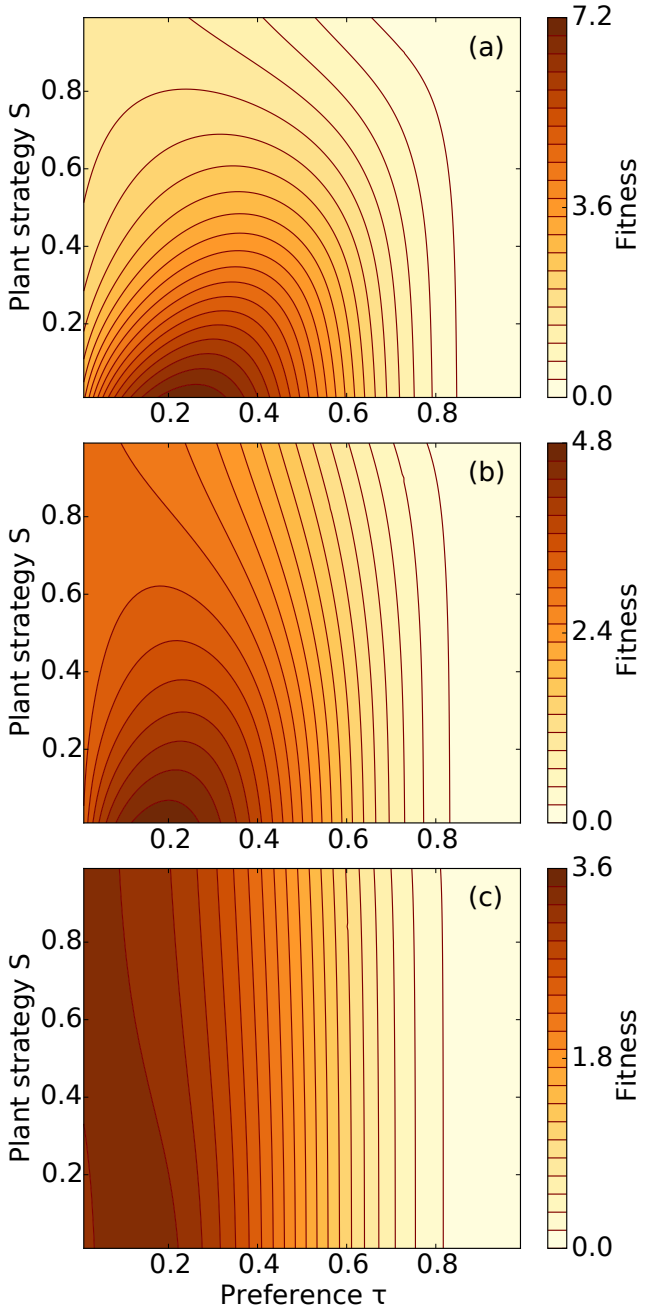

Figure 5.6.: Fitness of a herbivore population (i.e. mean number of offspring per herbivore individual reaching reproductive age; cp. Eq.(5.12)) in response to the plant strategy parameter S (cp. Eq.(5.5)) and herbivore preference τ (cp. Eq.(5.9)) using (a) the concave upwards, (b) the linear, and (c) the concave downwards performance function shown in Fig. 5.4.

with a scaling factor α. Thus, the mean fitness is

$$\overline{W}_H = \underbrace{\lambda_H \alpha}_{q} \Gamma(1-\beta) \int_0^{n_{\max}} \mathrm{d}n\, e^{-\frac{(n-\bar{n})^2}{2V_S}} \left(hn + cn^2\right)(\tau n + 1). \tag{5.26}$$

Again we substitute $b = \frac{1}{2V_S}$ and $x = n - \bar{n}$ leading to

$$\overline{W}_H = q\Gamma(1-\beta) \int_{-\tilde{x}}^{\tilde{x}} \mathrm{d}x\, e^{-bx^2} \left(h(x+\bar{n}) + c(x+\bar{n})^2\right)(\tau(x+\bar{n}) + 1). \tag{5.27}$$

The mass loss due to preference β is proportional to the preference τ, i.e. $\beta = \gamma\tau$, hence,

$$\begin{aligned}
\overline{W}_H =& q\Gamma(1-\gamma\tau) \int_{-\tilde{x}}^{\tilde{x}} \mathrm{d}x\, e^{-bx^2} \left(h(x+\bar{n}) + c(x+\bar{n})^2\right)(\tau(x+\bar{n}) + 1) \\
=& q\Gamma(1-\gamma\tau) \int_{-\tilde{x}}^{\tilde{x}} \mathrm{d}x\, e^{-bx^2} \big[(h\bar{n} + c\bar{n}^2)(\tau\bar{n} + 1) \\
&+ x\left((h + 2\bar{n}c)(\tau\bar{n} + 1) + \tau(h\bar{n} + c\bar{n}^2)\right) \\
&+ x^2\left(c(\tau\bar{n} + 1) + \tau(h + 2\bar{n}c)\right) \\
&+ x^3 c\tau\ \big].
\end{aligned} \tag{5.28}$$

Again, we use Eq.(5.15) to solve this integral. We find

$$\overline{W}_H = q(1-\gamma\tau)\left(W_0(\tau\bar{n} + 1) + \frac{c + \tau(h + 3c\bar{n})}{2b}\left(1 - 2\Gamma\tilde{x}e^{-b\tilde{x}^2}\right)\right). \tag{5.29}$$

Hence, for small variations around the mean nutrient level, i.e. around $\tilde{x} = 0$, for small curvature parameter c, and by keeping in mind that we consider small preferences τ, we find with $b = \frac{1}{2V_S} = \frac{S}{2(1-S)}$ (cp. Eq.(5.5)) that

$$\begin{aligned}
\overline{W}_H &= q\left(W_0(\tau(\bar{n} - \gamma) + 1) + \frac{c + \tau h}{2b}\right) \\
&= q\left(W_0(\tau(\bar{n} - \gamma) + 1) + \frac{(c + \tau h)(1-S)}{S}\right).
\end{aligned} \tag{5.30}$$

So, the fitness of a herbivore population having a linear performance function ($c = 0$) and preference for high-nutrient leaves ($\tau > 0$), increases with increasing plant nutrient level variability, which means with decreasing b or S. Under the assumption of a concave downwards performance function ($c < 0$), the herbivore population benefits from increasing plant nutrient level variability when it has considerable preference, namely when $\tau > \frac{|c|}{h}$. For $\tau = \frac{|c|}{h}$, herbivore fitness is independent of the plant strategy parameter S. When $c > 0$ (concave upwards function), the mean fitness increases with increasing plant nutrient level variability (i.e. decreasing S or b) independently of the extent of herbivore preference τ. Consequently, we find the same results as in Fig. 5.6.

Impact of a non-monotonically increasing performance function

Several empirical studies found that the nutrient performance function decreases for large nutrient levels (Fischer and Fiedler, 2000; Joern and Behmer, 1997, 1998; Zehnder and Hunter, 2009), such that the performance function has its maximum at an intermediate nutrient level and looks like a concave downwards parabola. Such a performance function implies that either excess nutrients lead to metabolic costs for their decomposition or that the nutrient level is correlated with another trait as for instance the secondary metabolites in a leaf (Tao et al., 2014). Furthermore, an increase in a specific nutrient concentration can lead to unbalanced food and thus to a

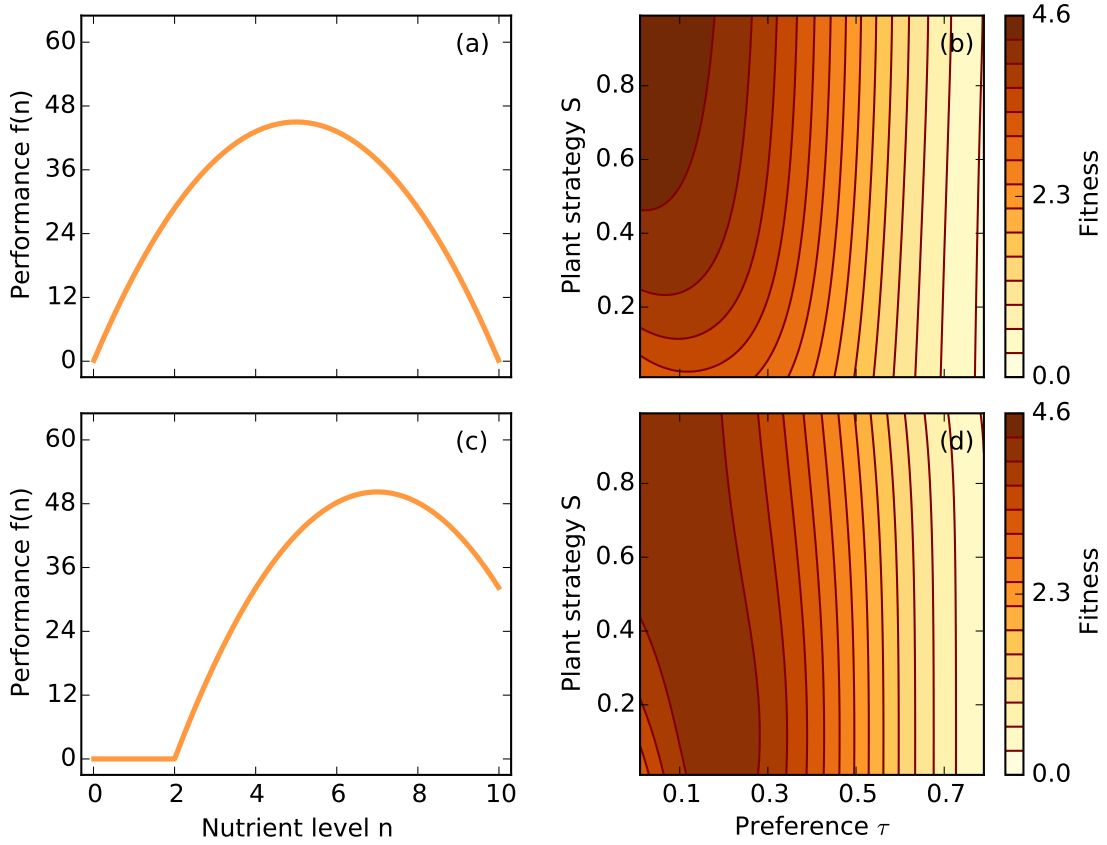

Figure 5.7.: (a), (c) The considered performance function having its maximum at an intermediate nutrient level: (a) $f_{\text{opt},1}(n) = \frac{9}{5}n(10-n)$, (c) $f_{\text{opt},2}(n) = \max\left(0, \frac{225}{112}\left(14n-24-n^2\right)\right)$. (b), (d) Herbivore fitness (i.e. mean number of offspring per herbivore individual reaching reproductive age; cp. Eq.(5.12)) displayed in color code in dependency of the plant strategy parameter S (i.e. the width of the nutrient level distribution; cp. Eq.(5.5)) and herbivore preference τ (cp. Eq.(5.9)) considering (b) $f_{\text{opt},1}$ and (d) $f_{\text{opt},2}$ as performance function.

lower performance (Tao et al., 2014). Here, we test the validity of our results under the assumption of such a non-monotonically increasing performance function.

For this investigation, we consider the performance functions shown in Fig. 5.7(a), (c) that differ in the location of the maximum. Again, we normalized the mean performance to 300 mg, i.e. $\int_0^{n_{\max}} f(n)\,\mathrm{d}n = 300$. Note, that the mean of the herbivore preference function is still located at the maximum of the corresponding fitness function, which coincides with the one of the performance function (cp. Eq.(5.8)). Hence, herbivores with $f_{\text{opt},1}$ prefer leaves with the mean nutrient level, i.e. $n = \bar{n} = 5$ (cp. Fig. 5.7(a)), and herbivores with $f_{\text{opt},2}$ prefer leaves with a nutrient level $n = 7.5$ (cp. Fig. 5.7(c)).

Fig. 5.7(b), (d) show the mean fitness of a herbivore population which responds to varying nutrient levels n as shown in Fig. 5.7(a), (c), respectively, in dependency of the plant strategy parameter S (cp. Eq.(5.5)) and the herbivore preference τ (cp. Eq.(5.9)).

The herbivore population always benefits from low plant nutrient level variability (i.e. large S, cp. Eq.(5.5)) when the maximum of the performance function coincides with the mean nutrient level (cp. Fig. 5.7(a), (b)) as illustrated by the color change from lighter to darker color with increasing S. This is the case since more leaves with the preferred nutrient level (which is $n = \bar{n} = 5$) are present with increasing S. Consequently, the herbivore only benefits from having preference when the nutrient level variability is broad (i.e. small S). Otherwise, herbivores having no preference reach the highest fitness, since the cost for finding even more leaves with the mean nutrient level exceeds the benefit when $S > 0.3$.

However, when the maximum of the performance function is not close to the mean nutrient level (cp. Fig. 5.7(c), (d)), the fitness landscape is qualitatively the same as those received with the monotonically

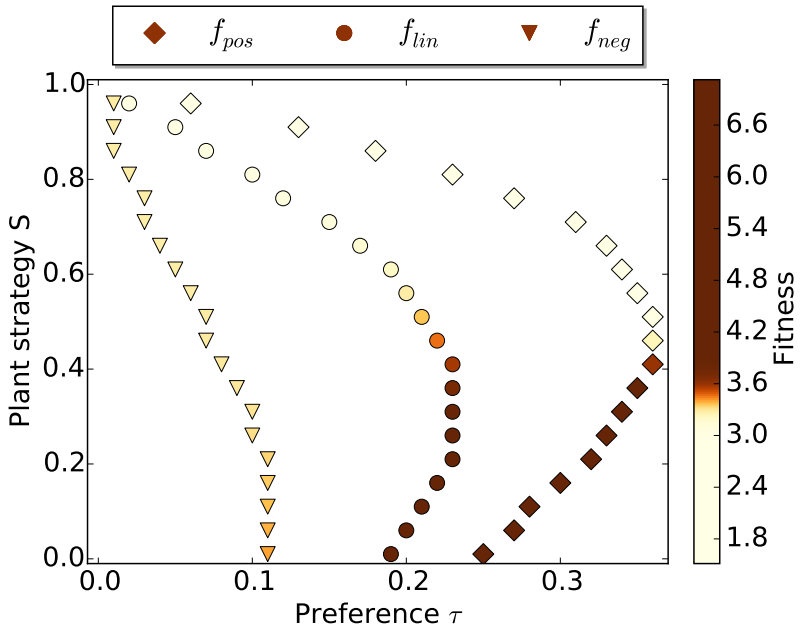

Figure 5.8.: Optimal preference, i.e. the preference that maximizes herbivore fitness, of a herbivore population that feeds on a plant with strategy parameter S (s. Eq.(5.5)) and has the concave upwards f_{pos} (diamonds), the linear f_{lin} (circle), and the concave downwards f_{neg} (triangles) performance function shown in Fig. 5.4. The color in the markers indicates the mean fitness of the herbivore population under the particular circumstances.

increasing concave downwards performance function f_{neg} (cp. Fig. 5.6(c)): a herbivore population, that has low preference ($\tau < 0.2$), suffers from a large nutrient level variability (i.e. small S), whereas a herbivore population that shows considerable preference ($\tau > 0.2$) benefits from small S.

Hence, our results of Section 5.4.4 are also valid when herbivores have a non-monotonically increasing performance function as long as its maximum does not coincide with the mean of the nutrient distribution $p(n)$, or is close to it.

Optimal herbivore preference

In the previous sections, we showed that herbivore preference can have crucial impact on the question whether a herbivore population benefits or suffers from large nutrient level variability. As herbivore preference is a strategy adaptable to the surrounding environmental conditions, the herbivore will evolve in an evolutionary process to the preference that maximizes its fitness. In this section, we investigate how this optimal preference depends on the curvature of the herbivore response function and the nutrient level variability.

Fig. 5.8 shows the optimal preference of a herbivore population that feeds on a plant with strategy parameter S (s. Eq.(5.5)) and has the concave upwards f_{pos} (diamonds), the linear f_{lin} (circle), and the concave downwards f_{neg} (triangles) performance function represented in Fig. 5.4. The markers' colors indicate the mean fitness of the herbivore population under the particular circumstances.

When nutrient level variability is large (i.e. small S), herbivores benefit from having an intermediate preference τ as such preference values suffice to considerably increase herbivore growth without implying too high costs.

The fitness of herbivores having optimal preference decreases with increasing plant strategy parameter S, i.e. with decreasing nutrient level variability, since herbivores can find more leaves with high nutrient levels when nutrient level variability is large (cp. Fig. 5.2(c), (d)).

Optimal preference is highest for the concave upwards performance function f_{pos}, followed by the linear f_{lin} and the concave downwards performance function f_{neg} independent of the plant strategy parameter S. This can be explained by taking a closer look at the performance functions. As the slope of the concave upwards performance function f_{pos} increases with the nutrient level, herbivore performance is low over a large range of nutrient levels compared to the whole considered nutrient level range. Hence, the benefit of herbivores to show preference when having this kind of performance function is higher than the benefit of herbivores having a concave upwards

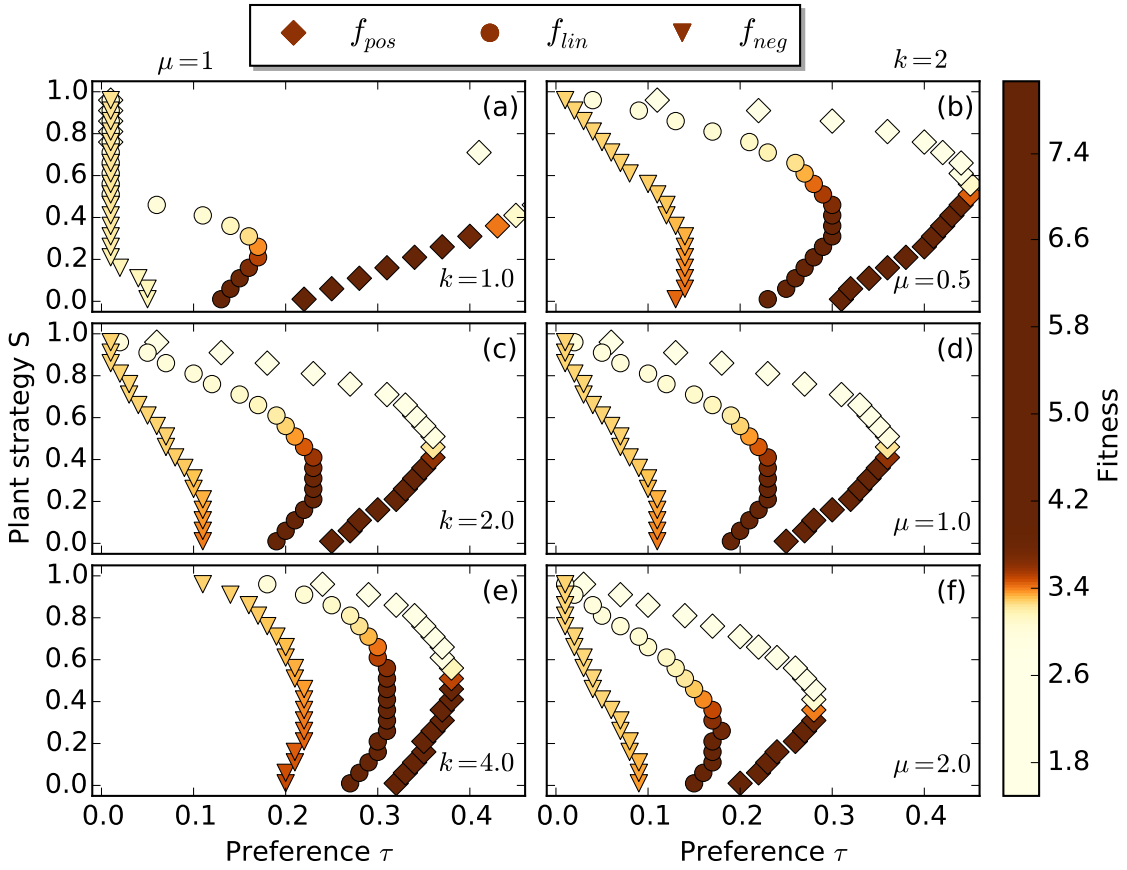

Figure 5.9.: Optimal preference, i.e. the preference that maximizes herbivore fitness, of a herbivore population that feeds on a plant with strategy parameter S (s. Eq.(5.5)) and has the concave upwards f_{pos} (diamonds), the linear f_{lin} (circle), and the concave downwards f_{neg} (triangles) performance function shown in Fig. 5.4. The parameters describing the costs for preference, μ, k (cp. Eq.(5.11)) vary between the different panels. In (a), (c), (e) k differs with $\mu = 1$; in (b), (d), (f) μ differs with $k = 2$. The color in the markers indicates the mean fitness of the herbivore population under the particular circumstances.

performance function (slope decreases with increasing nutrient level). Consequently, the strength of (optimal) herbivore preference depends on the curvature of the performance function and the plant strategy.

Further influences on the optimal herbivore preference

In this section, we identify further factors that influence optimal herbivore preference.

Costs for preference

First, we investigate the impact of the costs for preference on optimal preference of a herbivore feeding on a plant with strategy parameter S. We do this via altering the parameters that determine the shape of the mass loss due to preference, μ, k (cp. Eq.(5.11)).

Fig. 5.9 shows the optimal preference of a herbivore population feeding on a plant with strategy parameter S (s. Eq.(5.5)) that has the concave upwards f_{pos} (diamonds), the linear f_{lin} (circle), and the concave downwards f_{neg} (triangles) performance function shown in Fig. 5.4. In ((a), (c), (e)), we vary k and in ((b), (d), (f)) the parameter μ (cp. Eq.(5.11)). The color in the markers indicates the mean fitness of the herbivore population under the particular circumstances.

As in the previous section (cp. Fig. 5.8), herbivores having an intermediate preference reach the highest fitness when nutrient variability is large (i.e. $S = 0$) and herbivores having the concave upwards performance function

f_{pos} have the largest optimal preference followed by those having the linear performance function f_{lin}. Herbivores with the concave downwards performance function f_{neg} have the lowest optimal preference.

The fitness that is reached with optimal herbivore preference decreases with increasing S as in the previous section (cp. Fig. 5.8), apart from the case of a concave downwards performance function in Fig. 5.9(a). Here, it is not worth for the herbivore to have preference such that the herbivore increases with decreasing nutrient level variability due to the concave downwards performance function (cp. Fig. 5.5(c)).

With increasing parameter μ, optimal herbivore preference decreases for all performance functions used. The parameter μ determines the location of the half saturation maximum of the mass loss, i.e. the preference for which half of the mass is lost due to preference (cp. Fig. 5.3), i.e.

$$\tau_{\text{HSM}} = \frac{1}{\mu^{1/k} + 1}\,. \tag{5.31}$$

Hence, a larger μ implies higher costs for preference.

The parameter k has a more complex impact on optimal herbivore preference as it determines the slope in the half saturation maximum (s. Fig. 5.3). When optimal herbivore preference is considerably below the half saturation maximum, which is at $\tau_{\text{HSM}} = 0.5$ for all values of k (cp. Eq.(5.31) or Fig. 5.3), the herbivore population benefits from high values of k, since this includes lower costs (cp. Fig. 5.3). Consequently, optimal herbivore preference increases with increasing k when considering a concave downwards or a linear performance function. For the concave upwards performance function, this is true when the plant strategy parameter S (cp. Eq.(5.5)) is low or high. However, for intermediate values of the plant strategy parameter S, optimal herbivore preference is high (near the half saturation maximum) such that optimal herbivore fitness is higher when $k = 1$ than when $k = 2$. Nevertheless, herbivores having optimal herbivore preference are fitter when k is large.

Hence, the qualitative results found in the Section 5.4.4 are robust under changes of the parameters determining the costs for preference μ and k, but both parameters can considerably change the extent of optimal preference.

Magnitude of the curvature on optimal herbivore preference

We showed that the sign of the curvature has an impact on the strength of optimal herbivore preference. Consequently, the magnitude of the curvature might also have an impact. In this section, we test this hypothesis by considering two non-monotonically increasing concave upwards performance functions that differ in the magnitude of their curvature (s. Fig. 5.10(a), (c)). A performance function with a larger curvature is for instance suitable for more specialized herbivores that can only grow well on a smaller range of nutrient concentrations.

Fig. 5.10(b), (d) shows the mean fitness (cp. Eq.(5.12)) of a herbivore population in response to the plant strategy parameter S (cp. Eq.(5.5)) and herbivore preference τ (cp. Eq.(5.9)) using the functions shown in Fig. 5.10(a), (c) as performance function, respectively. The blue line indicates optimal preference, i.e. the preference that maximizes herbivore fitness for a given plant strategy parameter S.

The fitness landscapes do not differ qualitatively and show the typical behavior achieved when considering a concave downwards performance function: The herbivore population benefits from large nutrient level variability (i.e. small S) when herbivore preference is high, but the opposite is true when herbivore preference is low. Moreover, optimal herbivore preference is larger when the absolute value of the curvature of the performance function is larger as illustrated by the location of the blue line in Fig. 5.10(b) compared to (d). This is the case as the benefit of feeding on preferred leaves is larger when the performance function has the higher absolute curvature such that it is worth to take the higher costs for stronger preference (cp. Fig. 5.10(a), (c)).

In conclusion, not only the sign, but also the magnitude of the curvature of the performance function determines the extent of optimal herbivore preference.

5.4.5 Summary of major findings

Before discussing the results that we have found in this part of the chapter, we summarize the major findings regarding our research questions in Section 5.4.2:

- Nutrient level variability is *per se* beneficial for the plant when the herbivore has a concave downwards performance function and low preference or a concave downwards parabola performance function the optimum of which coincides with the mean nutrient level or is close to it.

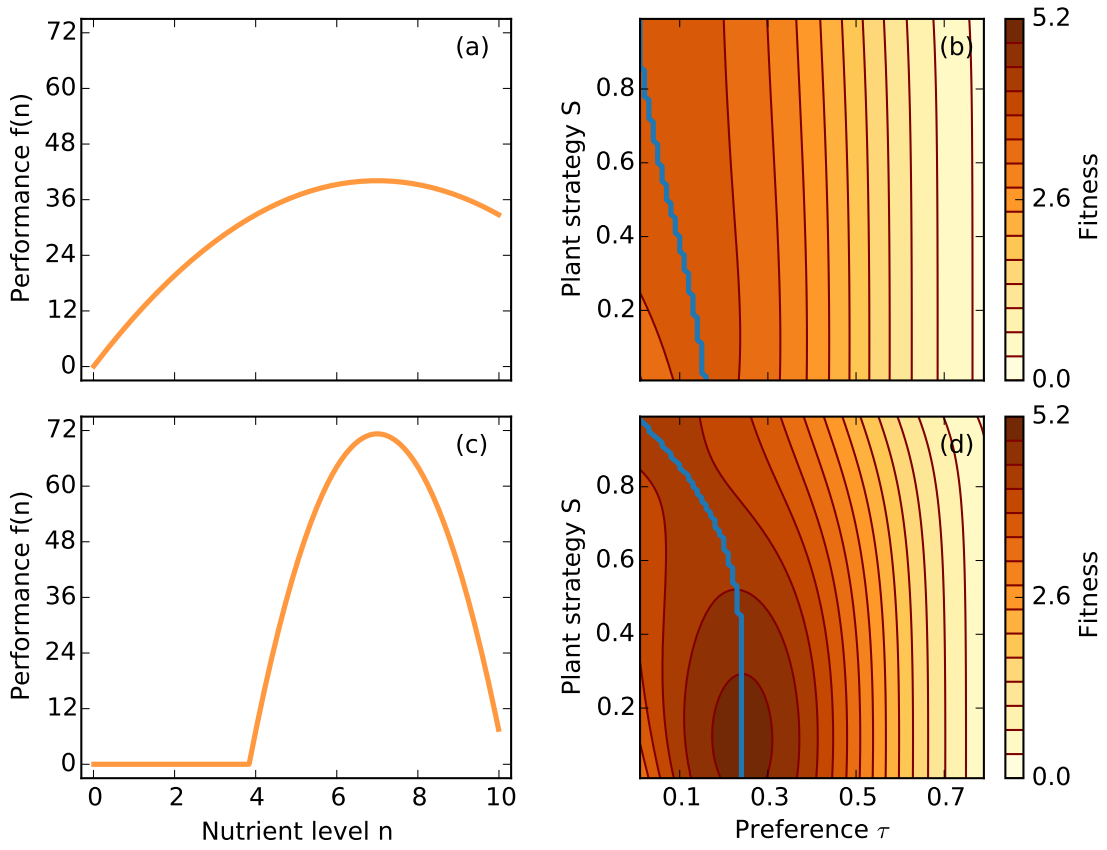

Figure 5.10.: (a), (c) The considered performance functions having their maximums at an intermediate nutrient level, $n = 7.5$. The performance functions differ in their curvature: (a) $f_{\text{opt,low}} = \frac{9}{11}(14n - n^2)$, (c) $f_{\text{opt,high}} = \max\left(0, \frac{900}{63+20\sqrt{10}}\left(14n - n^2 - 39\right)\right)$. (b), (d) Herbivore fitness (i.e. mean number of offspring per herbivore individual reaching reproductive age; cp. Eq.(5.12)) displayed in color code in dependency of the plant strategy parameter S (i.e. the width of the nutrient level distribution; cp. Eq.(5.5)) and herbivore preference τ (cp. Eq.(5.9)) considering (b) $f_{\text{opt,low}}$ and (d) $f_{\text{opt,high}}$ as performance function. The blue line indicates optimal preference, i.e. the preference that maximizes herbivore fitness for a given plant strategy parameter S.

- The herbivore benefits from having stronger preference when:
  1. The costs for preference are low.
  2. Nutrient level variability is high or intermediate (depending on the costs).
  3. The nutrient level range, where the herbivore can grow well, is small and not around the mean nutrient level. The strength of preference thus depends on the magnitude and the sign of the curvature of the performance function.

5.4.6 Discussion

In this section, we investigated the *per se* effect of nutrient level variability on a plant-herbivore system and in particular we focused on the impact of herbivore preference on these results. When the plant *per se* benefits from nutrient level variability because of a herbivore that is less fit, this may be one reason for the enormous extent of nutrient level variability found in nature (Herrera, 2009; Siefert et al., 2015). The model and the results are valid when considering intra- or inter-individual nutrient level variability as well as feeding or oviposition preference.

For our investigation, we chose monotonically increasing herbivore performance functions with different curvatures in order to take for instance different nutrients, nutrient level ranges (Miles et al., 1982; Ohmart et al., 1985), and herbivores of diverging ages (Ohmart et al., 1985; Montgomery, 1982; Scriber and Slansky Jr, 1981) into account. Such monotonically increasing performance functions are appropriate when excess nutrients do not include negative effects, e.g. because the nutrient level describes the food quality from the herbivores' point of view. If this is not a valid assumption, nutrient performance functions that look like a concave downwards parabola are a good consideration as found in multiple studies (Zehnder and Hunter, 2009; Joern and Behmer, 1998; Fischer and Fiedler, 2000; Joern and Behmer, 1997; Boersma and Elser, 2006). Hence, we additionally tested the validity of our results in this case.

Following Jensen's inequality, the *per se* effect of nutrient level variability crucially depends on the curvature of the herbivore performance function (Wetzel et al., 2016; Ruel and Ayres, 1999) (s. Section 5.1). Indeed, in the case of no herbivore preference, we found that large nutrient level variability is *per se* beneficial for herbivores when having a concave upwards performance function, but disadvantageous under the assumption of a concave downwards one. When the herbivore performance function is linear, nutrient level variability has no impact on herbivore fitness. This corresponds to the implications of Jensen's inequality as well as the results of previous studies (Wetzel et al., 2016; Ruel and Ayres, 1999) and we showed analytically that the results of our model are, in this case, reducible to Jensen's inequality. In their meta-study, Wetzel et al. (2016) indeed found that the nutrient performance function is in average concave downwards which may be a reason for the large nutrient level variability in plants.

However, we showed that the inclusion of herbivore preference in our model can considerably alter the *per se* impact of nutrient level variability. More precisely, we find that herbivores, having strong preference for high nutrient level leaves, benefit from large nutrient level variability independently of the curvature of herbivore performance function. The reason is that the herbivores prefer leaves with high nutrient concentrations that occur less frequently with decreasing nutrient level variability. This is only invalid when considering a performance function that has the form of a concave downwards parabola, the maximum of which is close to the mean nutrient level. In this case, the fraction of leaves preferred by the herbivores (i.e. containing the mean nutrient concentration) increases with decreasing nutrient level variability around this mean nutrient concentration and thus enables higher growth rates of the population. These results are robust under changes of the preference mean as long as herbivores still prefer high-quality leaves. Otherwise, it is not worth to show preference.

Due to the crucial impact of herbivore preference on the *per se* effect of nutrient level variability, we further focused on the preference, more precisely on optimal herbivore preference. Optimal preference is the preference that maximizes herbivore fitness for a given plant strategy parameter S. In an evolutionary process, the herbivore will evolve to this optimal preference. We find that optimal herbivore preference depends on (i) the plant strategy parameter S (i.e. the nutrient level variability), (ii) the sign and the magnitude of the curvature of herbivore performance function, and (iii) the costs for preference.

Indeed, we find empirical evidence for these dependencies: Studies suggest that a higher herbivore preference includes a longer time of searching appropriate food, such that there is a trade-off between the number of eggs laid (i.e. costs for preference) and time spent searching for appropriate sites and thus preference (Wiklund and Persson, 1983). Furthermore, it is found that herbivore preference is stronger when high-quality leaves are rare (Tilmon, 2008). This is in agreement with our findings, that optimal herbivore preference increases with decreasing

nutrient level variability as long as variability is not too low. However, such a low nutrient level variability may be an unrealistic scenario in nature anyway (Siefert et al., 2015; Herrera, 2009). We found this dependency under the assumption of a concave upwards or a linear performance function and for a concave downwards performance function when the costs for preference are low (s. Fig. 5.9). Furthermore, some studies found that specialists have a stronger preference than generalists (Gripenberg et al., 2010; Tilmon, 2008; Soto et al., 2012). Since generalists feed on multiple host plant families, they should be able to deal well with a wider range of nutrient concentrations (e.g. because of a concave downwards performance function) than specialists.

Even when nutrient level variability is *per se* beneficial for a herbivore as showing considerable preference or having a concave upwards performance function, this does not necessarily mean that the plant suffers from large nutrient level variability. Nutrient level variability may be beneficial for the plant for other reasons than herbivory. For instance, Kotowska et al. (2010) found that plant genetic diversity increases plant survival and biomass, both in the presence and absence of herbivores, whereby the percentage increase was lower in the presence of the herbivore. Kotowska et al. (2010) further found that the increase in plant biomass and survival in genetic mixtures was non-additive and could thus not be explained by averaging the results of the corresponding monocultures. One explanation for these findings may be that different resource uptake strategies decrease intraspecific competition in genetic mixtures (Kotowska et al., 2010; Crutsinger et al., 2006). Furthermore, different herbivores may prefer leaves with different traits, for instance because of differing specialization strategies (generalist vs. specialist) (Gutbrodt et al., 2012) or as a response to drought and associated changes in secondary defense compounds (Gutbrodt et al., 2011). In this case, large nutrient level variability is also *per se* beneficial for the plant since in average, the herbivores have low preference. Additionally, and besides such effects that show bottom-up control, the herbivores may be also regulated by top-down control, i.e. by higher trophic levels (Singer et al., 2012). In this study, we neglected higher trophic levels since we want to distill the *per se* impact of intraspecific trait variability on herbivore fitness.

In a nutshell, we showed that nutrient level variability is *per se* beneficial for a plant when its herbivores have a concave downwards performance function and show low preference, for instance because of high costs for preference. However, when the herbivores have considerable preference, the plant does not *per se* benefit from large nutrient level variability, but as discussed above, this does not necessarily mean that large nutrient level variability is not the best plant strategy in complex ecosystems.

Finally, with regard to the findings of Section 3 showing that the predator can benefit from prey defense since the increase of prey density and the resulting higher consumption rate outweigh the decrease in this quantity due to the higher fraction of defended prey, the *per se* effect of nutrient level variability on the herbivore may also change when we do not consider that the plant population is high. In this case, we need to simulate both the herbivore and the plant population. Indeed, when the herbivore population is limited by the available plant biomass, has low preference, and a concave downwards performance function, it also benefits from low nutrient level variability like the plant (s. Appendix H).

5.5 Influence of plant defense level variability on the fitness of specialist and generalist herbivores

Plant defense or resistance is another example of a plant trait that is known to differ on all organization levels of intraspecific trait variability as defined in the beginning of this Chapter 5 (Denno, 2012; Herrera, 2009; Siefert et al., 2015). Plant defense reduces the herbivore damage (Karban et al., 1997) and is an important strategy for plants due to their immobility (Karban and Baldwin, 2007; Gutbrodt et al., 2012; Karban and Agrawal, 2002). Plants have even evolved different defense mechanisms, namely, permanent constitutive defenses such as thorns, trichomes[10] (Lankau, 2007; Karban and Baldwin, 2007), secondary metabolites[11] (Gutbrodt et al., 2012; van der Meijden, 1996; Dimarco et al., 2012; Karban and Baldwin, 2007), or a higher toughness of the leaves (Clissold et al., 2009; Dimarco et al., 2012; Karban and Baldwin, 2007) and (ii) temporary, inducible defense (Karban and Baldwin, 2007) (cp. introduction of Chapter 3). The defensive traits underlying either of these defensive mechanisms can vary spatially and temporally in their amount or extent (Karban et al., 1997; Herrera, 2009; Siefert et al., 2015), but on different temporal scales.

The ability to deal with plant defense considerably differs among herbivores – specialists have adapted to their host plant family, i.e. also to their defense mechanisms, such that they can cope with a large range of plant defense levels in contrast to generalists (Lankau, 2007; Kliebenstein et al., 2002; Siemens and Mitchell-Olds, 1996; Poelman et al., 2008a; Schoonhoven et al., 2005). Some specialists even have evolved offensive traits (Karban and Agrawal, 2002) as for instance the ability to convert consumed plant defense into proper defense against predators (Dimarco et al., 2012; Despres et al., 2007). These sequestering specialists thus benefit from consuming leaves with a non-zero defense level (Dimarco et al., 2012; Despres et al., 2007). In contrast, generalists are effectively deterred by the plant defense and can only grow well on weakly or undefended leaves (Lankau, 2007; Kliebenstein et al., 2002; Siemens and Mitchell-Olds, 1996; Poelman et al., 2008a; Schoonhoven et al., 2005). Consequently, the *per se* effect of defense level variability may differ for herbivores with different specialization degrees.

Multiple studies investigated how plant response differs under generalist or specialist attacks (Lankau, 2007; Ali and Agrawal, 2012; Agrawal, 2000; Tollrian and Harvell, 1999; Karban et al., 1997; Gutbrodt et al., 2012). As a consequence, several studies focused on the optimal plant defense under attack of both generalists and specialists (optimal defense theory) (van der Meijden, 1996). However, little is known about the *per se* impact of defense level variability and so about the best plant strategy when the mean defense level is kept constant. In particular, the impact of herbivore preference on the best plant strategy is poorly understood, although we showed in the previous Section 5.4 that (the extent of) herbivore preference is a crucial factor for answering this question. Furthermore, specialists and generalists may differ in the extent of their preference behaviour (van Leur et al., 2008).

In this section, we thus investigate under which conditions the plant *per se* benefits from large defense level variability that is attacked by either generalist or sequestering or non-sequestering specialist herbivores. In order to ensure that the sequestering specialist can make use of its ability to convert consumed plant defense, we consider that the herbivores suffer loss due to predation. In particular, we again focus on the impact of herbivore preference and additionally on the influence of this predation pressure on our results. Since young leaves often contain higher defense and nutrient concentrations than old leaves (Blüthgen and Metzner, 2007; Gutbrodt et al., 2012), we additionally investigate the impact of a relationship between the defense and the nutrient level of a leaf on our results. Tao et al. (2014) proposed that such a correlation may explain a performance function that looks like a concave downwards parabola. Since we found in the previous Section 5.4 that trait variability may be *per se* beneficial for the plant independently of herbivore preference for such a performance function[12] (cp. Fig. 5.7), this is a promising approach to explain the enormous extent of defense and nutrient level variability in plants (Denno, 2012; Herrera, 2009; Siefert et al., 2015).

5.5.1 Specification of the model

For this study, we need to define/introduce three aspects:

- A performance function that represents the growth of a generalist, a sequestering, and a non-sequestering specialist, respectively by an appropriate choice of parameter values.

[10] These are small hair-like structures that can in principle fulfill different functions in an organisms (Mauricio and Rausher, 1997).

[11] Secondary metabolites are chemical substances that are generally attributed a defense function. It appears that they play no role in the pathways of the plant's normal biochemical synthesis (Begon et al., 1997).

[12] More precisely, we found that the plant benefits from nutrient level variability when the performance function has its maximum near the mean nutrient level.

- The possibility to consider different extents of nutrient level variability.
- The probability to be consumed by a predator in order to ensure that sequestering plant defense has some use.

We introduce these extensions in the following.

Correlation between the defense and the nutrient level

We assume a linear correlation between the defense and the nutrient level of a leaf. Furthermore, we choose a function that allows us to consider different extents of nutrient level variability for a given defense interval. A simple realization is

$$n(d) = n(\bar{d}) + l(d - \bar{d}), \tag{5.32}$$

which means that the nutrient level varies in $n \in [n(\bar{d}) - l\bar{d}; n(\bar{d}) + l\bar{d}]$ and the correlation parameter l determines to which extent undefended and strongly defended leaves differ in their nutrient level. For $l = 0$, all leaves have the same nutrient concentration and the higher l, the larger is the nutrient level variability. Denoting the defense level distribution as $p_d(d)$, the nutrient level distribution is

$$p_n(n) = \frac{1}{l} p_d(d(n)) = \frac{1}{\sqrt{2\pi V_S l^2}} e^{\frac{(n(d)-n(\bar{d}))^2}{2V_S l^2}}. \tag{5.33}$$

Performance function

The performance function is a crucial factor to distinguish the different herbivore strategies. We assume that the herbivore performance on undefended leaves is described by the nutrient performance function $f_n(n)$ in dependency of the nutrient level n in the considered leaf. We further assume that this performance is diminished for increasing plant defense level d independent of whether we consider generalist or specialist herbivores (Ali and Agrawal, 2012). The performance decrease arises due to costs for removing the defense material or for converting it into proper defense (Ali and Agrawal, 2012). However, the amount of these costs considerably differs with the herbivore specialization strategy (Ali and Agrawal, 2012). Thus, we define the performance function $f(d)$ as

$$f(d) = f_n(n(d))[1 - g(d, \nu)], \tag{5.34}$$

where $g(d, \nu) \in [0, 1]$ describes the proportional growth deficiency in dependency of the defense level d of the consumed leaf. The parameter ν models the costs for removing or converting consumed plant defense and in the following, we will refer to the latter as cost factor ν. The cost factor ν forms the performance function in dependency of the defense level in a leaf and has thus a major contribution to distinguish generalist, sequestering, and non-sequestering specialist herbivores. In the following, we describe the nutrient performance function $f_n(n)$ and the proportional growth deficiency $g(d, \nu)$ in detail.

Nutrient performance function

We assume that generalists and specialists differ in their ability to deal with undefended leaves, more precisely, we consider that the performance of a specialist and a generalist herbivore on a leaf with nutrient level n differ by a factor γ, i.e.

$$f_n(n) = \gamma f_n^{\text{Spec}}(n). \tag{5.35}$$

In order to ensure that it is beneficial to be a generalist under some conditions, we assume that the generalist performs better on undefended leaves, i.e.

$$\gamma = \begin{cases} 1, & \text{if specialist,} \\ \gamma_{\text{Gen}} > 1, & \text{if generalist.} \end{cases} \tag{5.36}$$

In the following, we refer to the parameter γ as generalist benefit factor. Note, that this assumption does not affect our results qualitatively.

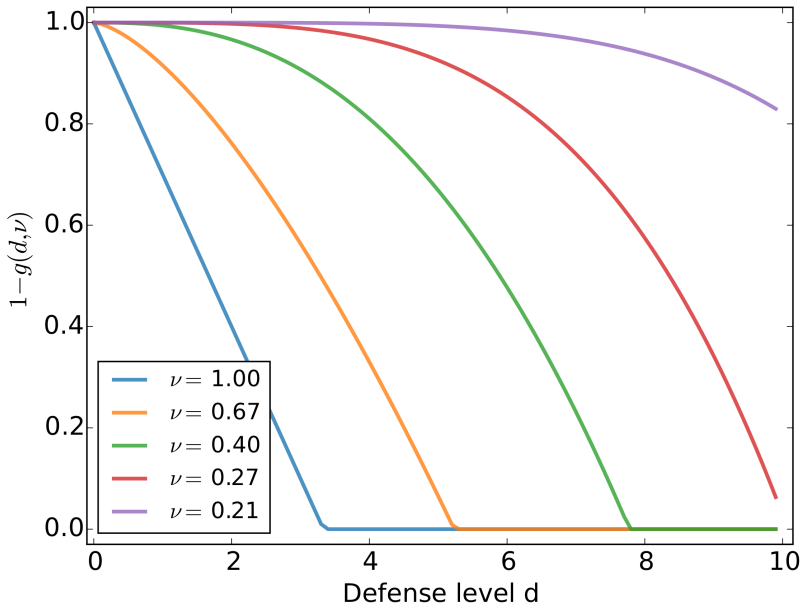

Figure 5.11.: The proportional growth deficiency, $g(d, \nu)$, represented as $1 - g(d, \nu)$ and plotted for different cost factors ν.

Proportional growth deficiency

Numerous studies have found that many specialists have evolved effective mechanisms to sustain the defenses of their hosts, while generalists are efficiently deterred by plant defenses (Lankau, 2007; Kliebenstein et al., 2002; Siemens and Mitchell-Olds, 1996; Poelman et al., 2008a). To find an appropriate function for the proportional growth deficiency $g(d, \nu)$, we thus assume that $g(d, \nu)$ should be a slowly increasing function for small defense levels considering specialized herbivores (Ali and Agrawal, 2012), i.e. a concave upwards function, and a faster increasing function for generalist herbivores (Ali and Agrawal, 2012), hence a linear or concave downwards function. Note, that the performance function is proportional to $1 - g(d, \nu)$ and has consequently the opposite curvature.

Furthermore, for a generalist, $g(d, \nu)$ should reach one at a smaller defense level d than for a sequestering specialist herbivore, followed by a non-sequestering specialist herbivore. The latter includes that sequestering specialists need to take higher costs for the ability to convert consumed plant defense than non-sequestering specialists (Björkman and Larsson, 1991). A simple function that satisfies these assumptions with an appropriate choice of parameter values is

$$g(d, \nu) = \max\left[\left(3.75 - \frac{0.75}{\nu}\right)\left(\frac{d}{d_{\max}}\right)^{\nu}, 0\right], \tag{5.37}$$

with the maximal considered defense level $d_{\max}$ and the cost factor $\nu \geq 0.2$. Fig. 5.11 shows the behavior of the function $1 - g(d, \nu)$ for varying cost factors ν. We tested other variants to describe the proportional growth deficiency $g(d, \nu)$, but this did not affect the results qualitatively (s. Appendix G).

Probability to be consumed by a predator

In order to ensure that sequestering specialists can benefit from their ability to convert consumed plant defense into own defense, we consider that herbivores suffer loss by predation. Thereby, we assume that the converted defense material is directly noticed by the predator, for instance, through an altered appearance of the herbivore. Such alerting signals may involve specific colors and odors sequestered from their specific host plants (Nishida, 2002). Hence, sequestered defense directly decreases the probability to be consumed $a(d)$. Additionally, in the population average, this can be caused by a learning process of the herbivores. Hence, including the probability to be consumed $a(d)$ in Eq.(5.8) for the fitness of a herbivore individual feeding on a leaf with defense level d yields

$$W_H(d) = \lambda_H f(d)(1-a(d))$$
$$\overset{(5.34)}{=} \lambda_H f_n(n(d))[1-g(d,v)](1-a(d)). \tag{5.38}$$

In order to find an appropriate expression for the probability to be consumed $a(d)$, we denote the predator encounter rate as a_0. We multiply a_0 with a function of the plant defense d that describes that the probability to be consumed by a predator can be reduced when the herbivore is able to sequester defense. Since we want to explore the effect of converted plant defense, we use a function that allows us to interpolate between 0 and 1 in different ways by changing the parameter of this function. A simple example is

$$a(d) = \frac{a_0}{1+\theta d}, \tag{5.39}$$

with the efficiency of converting plant defense θ. So, a general definition of the efficiency of converting plant defense θ is

$$\theta = \begin{cases} \theta_s, & \text{if sequestering} \\ 0, & \text{else}. \end{cases} \tag{5.40}$$

We also tested other functions to model the loss due to predation which led to the qualitative same results (s. Appendix G).

The mean fitness of a herbivore population consisting of generalists, sequestering, or non-sequestering specialists thus changes from the expression in Eq.(5.12) to

$$\overline{W}_H(d) = \Gamma\lambda_H(1-\beta)\int_0^{d_{\max}} \mathrm{d}d\, \Phi_p(d)p(d)f(d)(1-a(d))$$
$$= \Gamma\lambda_H(1-\beta)\int_0^{d_{\max}} \mathrm{d}d\, \Phi_p(d)p(d)f_n(n(d))[1-g(d,v)](1-a(d)), \tag{5.41}$$

whereby the different herbivore specialization strategies differ in the choice of the cost parameter v, the generalist benefit factor γ (via $f_n(n(d))$; cp. Eq.(5.35)), and the efficiency of converted defense θ (via $a(d)$; cp. Eq.(5.39)).

Here, the fitness $W_H(d)$ of a herbivore individual feeding on a leaf with defense level d can have a different functional form than the performance function $f(d)$ due to the probability to be consumed $a(d)$ (cp. Eq.(5.38)). Hence, sequestering specialists may prefer leaves on which they do not reach their performance maximum. As some studies found that herbivores prefer oviposition on leaves on which they have a high performance (Via, 1986; Herrera, 2009; Tabashnik et al., 1981; Travers-Martin and Müller, 2008; Despres et al., 2007; Rausher, 1979), we tested whether our results change when we choose the performance maximum as preference mean (instead of the fitness maximum). However, we found the qualitatively same results.

Choice of parameter values

In our study, we vary the defense level $d \in [0, 10]$. We further assume that leaves with the mean defense level contain a nutrient level $n(\bar{d}) = \bar{d} = 5$, such that the nutrient level varies in $[\bar{d}(1-l); \bar{d}(1+l)]$, with $l \in [0, 1]$ (cp. Eq.(5.32)). Note, that each interval can be mapped onto this one by choosing a suitable correlation parameter l and appropriate units for the defense and the nutrient level similar to the previous section.

For all parameters that reoccur in this study, we assume the same values as in the previous section (cp. Section 5.4.1) – they are listed in Tab. 5.1(b). The parameters that distinguish the different herbivore strategies are listed in Tab. 5.1(a). We assume that the generalist can grow twice as fast on undefended leaves than the specialists, but has to take the highest costs for dealing with plant defense. Sequestering specialists have the ability to convert plant defense and thus have a non-zero efficiency of converting defense θ_S. Note, that the choice of the generalist benefit factor γ does not qualitatively change the results.

Table 5.1.: Parameter values used for distinguishing the different herbivore strategies (Tab. 5.1(a)) and the remaining parameter values of the model (Tab. 5.1(b)).

(a) Parameters used to distinguish the different herbivore strategies, i.e. being a generalist, non-sequestering, or sequestering specialist.

	Generalist	**Non-seq. specialist**	**Seq. specialist**
Cost parameter ν	1	0.27	0.4
Generalist benefit factor γ	2	1	1
Efficiency of converting defense θ_S	0	0	10

(b) Remaining parameter of the model. The cost parameter for preference are defined in Eq.(5.11).

Number of offspring reaching reproductive age per growth unit	**Cost parameter for preference**	**Cost parameter for preference**
λ_H	μ	k
$0.01\,\frac{1}{\text{mg}}$	1	2

For the nutrient performance function $f_n(n)$, we use a concave downwards function as found in the meta-study of Wetzel et al. (2016). More precisely, we use the concave downwards function f_{neg} of the previous section, which is shown in Fig. 5.4 and 5.12. As in the previous section, we normalize the mean performance of the specialist herbivores concerning the nutrient concentration in the leaves to 300 mg, i.e. $\int f_n^{\text{Spec}}(n)\text{d}n = 300$. The marked areas in Fig. 5.12 show the range in which the nutrient performance function varies considering a correlation parameter $l \in \{0; 0.5; 1\}$.

Fig. 5.13 shows the resulting performance functions as well as the fitness $W_H(d)$ of a herbivore individual feeding on a leaf with defense level d (and thus nutrient level $n(d)$) for varying predator encounter rate a_0 ((b), (d), (f)) and correlation parameter l ((a), (c), (e)). According to Jensen's inequality (s. Section 5.1), the specialist herbivores suffer from large defense level variability as having concave downwards performance functions. The generalist has a linear performance function when $l = 0$, which means that defense level variability has no impact on herbivore fitness following Jensen's inequality. However, for $l > 0$, the performance function of the generalist herbivore is also concave downwards such that the generalist suffers from large defense level variability in this case according to Jensen's inequality (cp. Fig. 5.13)(c), (e))[13].

5.5.2 Research questions

We divide our investigation into two parts. First, we distill the *per se* impact of defense level variability on herbivore fitness, which means that we assume that the nutrient concentration is equal in all leaves and has thus no impact on the herbivore. Here, we want to investigate the following questions:

- Is defense level variability *per se* beneficial for a plant that is attacked by specialist or generalist herbivores?
- Does the *per se* impact of defense level variability change when herbivores evolve to optimal preference?
- What is the impact of the predator encounter rate a_0 on these results?

In the second part, we assume that the defense level of a leaf is correlated with its nutrient concentration and so we ask:

- What is the impact of a correlation between the defense and the nutrient level of a leaf on the results of the previous part?

In the following, we present our results concerning these research questions.

[13] Note, that the performance function of the generalist herbivore only differs by a constant factor from the fitness $W_H(d)$ of a generalist individual feeding on a leaf with defense level d (cp. Eq.(5.38)).

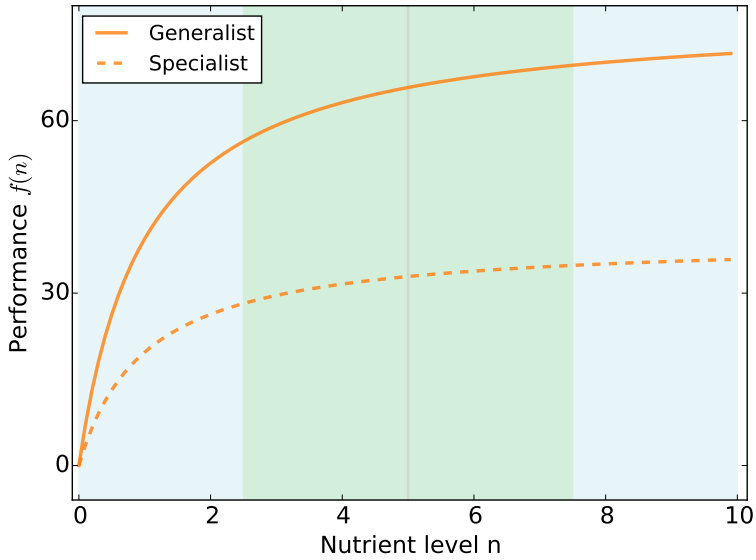

Figure 5.12.: Nutrient performance function for generalist and specialist herbivores: $f_{\text{neg}}(n) = \frac{300}{10-\ln(11)} \frac{n}{n+1}$. The marked areas show the considered nutrient level interval for $l \in \{0; 0.5; 1\}$.

5.5.3 Equal nutrient concentration in all leaves

First, we assume that the plant leaves only differ in their defense level in order to distill the effect of defense level variability. This means that we choose a correlation parameter $l = 0$ (cp. Eq.(5.32)). In particular, we are interested in the influence of herbivore preference τ (cp. Eq.(5.9)) and the predator encounter rate a_0 (cp. Eq.(5.39)) on herbivore fitness. When the predator encounter rate a_0 is non-zero, the sequestering specialist prefers weakly defended leaves compared to undefended leaves (s. Fig. 5.13(b), (d), (f)), while the latter are preferred by generalist and non-sequestering specialists (s. Fig. 5.13(b), (d), (f)).

Fig. 5.14 shows the mean fitness (cp. Eq.(5.41)) of a herbivore population consisting of generalists, non-sequestering, or sequestering specialists in response to the plant strategy parameter S (cp. Eq.(5.5)) and herbivore preference τ (cp. Eq.(5.9)) for different predator encounter rates a_0. The blue line indicates optimal herbivore preference, i.e. the preference that maximizes herbivore fitness for a given plant strategy parameter S. The white region shows where the fitness of the herbivore is lower than one, which means that the herbivore population would go extinct in the long-term limit.

First, we check the validity of our results of the previous Section 5.4. Optimal preference is largest for the generalist herbivore followed by the sequestering and the non-sequestering specialist as indicated by the blue lines in Fig. 5.14. This is in line with our conclusions of the previous Section 5.4 that optimal preference increases, when the trait range, where the herbivore can grow well, decreases (cp. Section 5.4.5).

Furthermore and similar to our findings of Section 5.4.4, we find that specialists with low preference benefit from low defense level variability (i.e. large S) due to the concave downwards performance function, but suffer from this situation when they have high preference. This is indicated by the color change from darker to lighter color with increasing S when approximately $\tau > 0.05$ (sequestering specialist) or $\tau > 0.1$ (non-sequestering specialist) in Fig. 5.14 that reverses for a lower preference. However, the generalist herbivore benefits from high defense level variability (i.e. small S) independently of its preference τ despite of its linear performance function. In this case, our results from the previous Section 5.4.4 would predict that defense level variability has no impact on the fitness of a herbivore that has no preference (i.e. $\tau = 0$) following Jensen's inequality (cp. Fig. 5.5(b)). The performance function of the generalist herbivore, however, decreases fast and is zero over a wide range of the considered defense level interval. Hence, it can be approximated by a concave upwards performance function, for which we indeed found in the previous Section 5.4.4 that the herbivore benefits from large defense level variability independently of herbivore preference (cp. Fig. 5.6(a)). These findings are independent of the predation pressure a_0.

This means that a plant, that is attacked by specialists with low preference, benefits from large defense level variability, but suffers from large defense level variability when being consumed by generalists or specialist herbi-

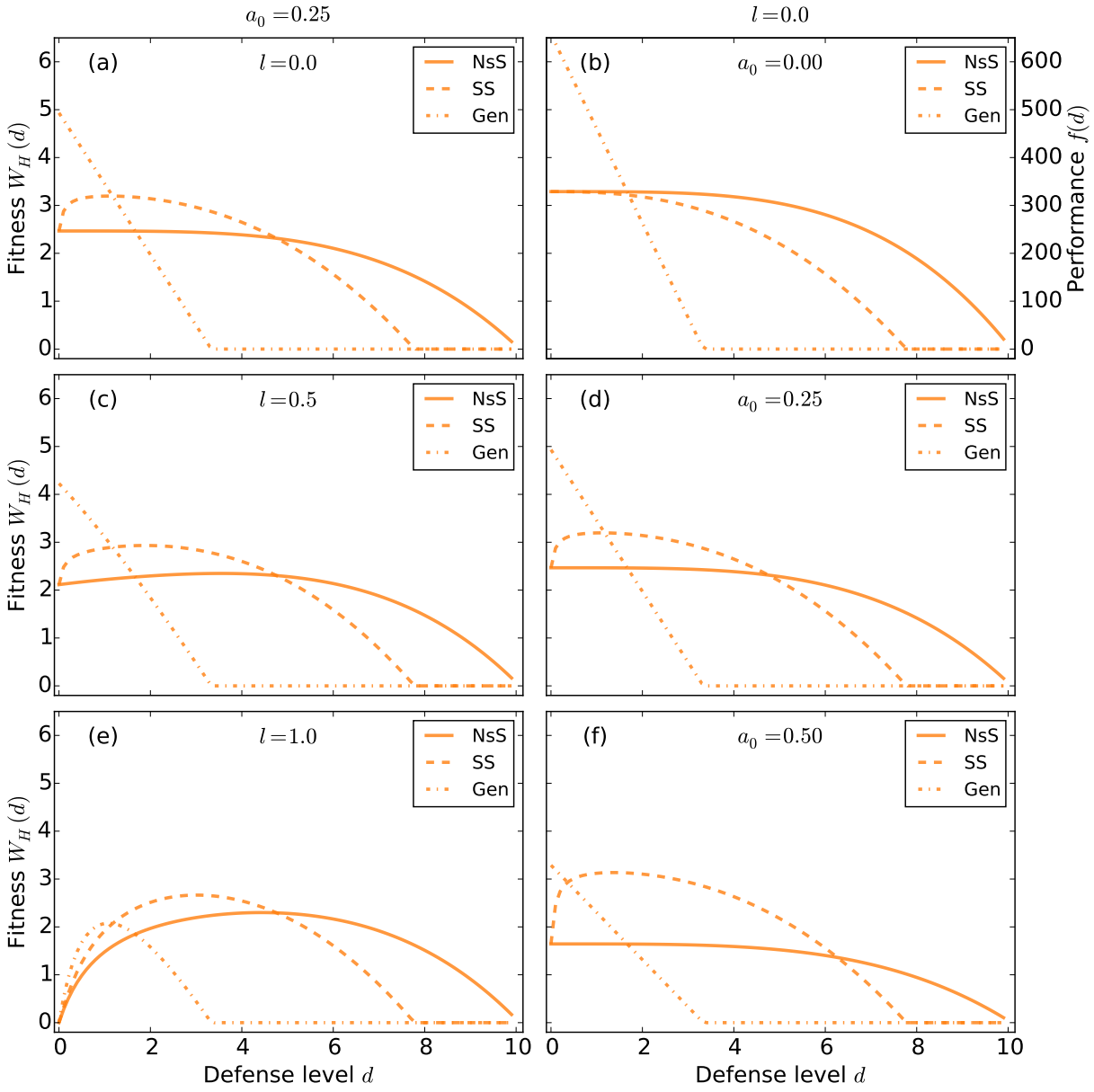

Figure 5.13.: Performance $f(d)$ and fitness $W_H(d)$ of a generalist (Gen), sequestering (SS), and non-sequestering specialist (NsS) individual feeding on a leaf with defense level d for different predator encounter rates a_0 (cp. Eq.(5.39)) and a correlation parameter $l = 0$ in (b), (d), (f) and different correlation parameters l (cp. Eq.(5.32)) and a predator encounter rate $a_0 = 0.25$ in (a), (c), (e).

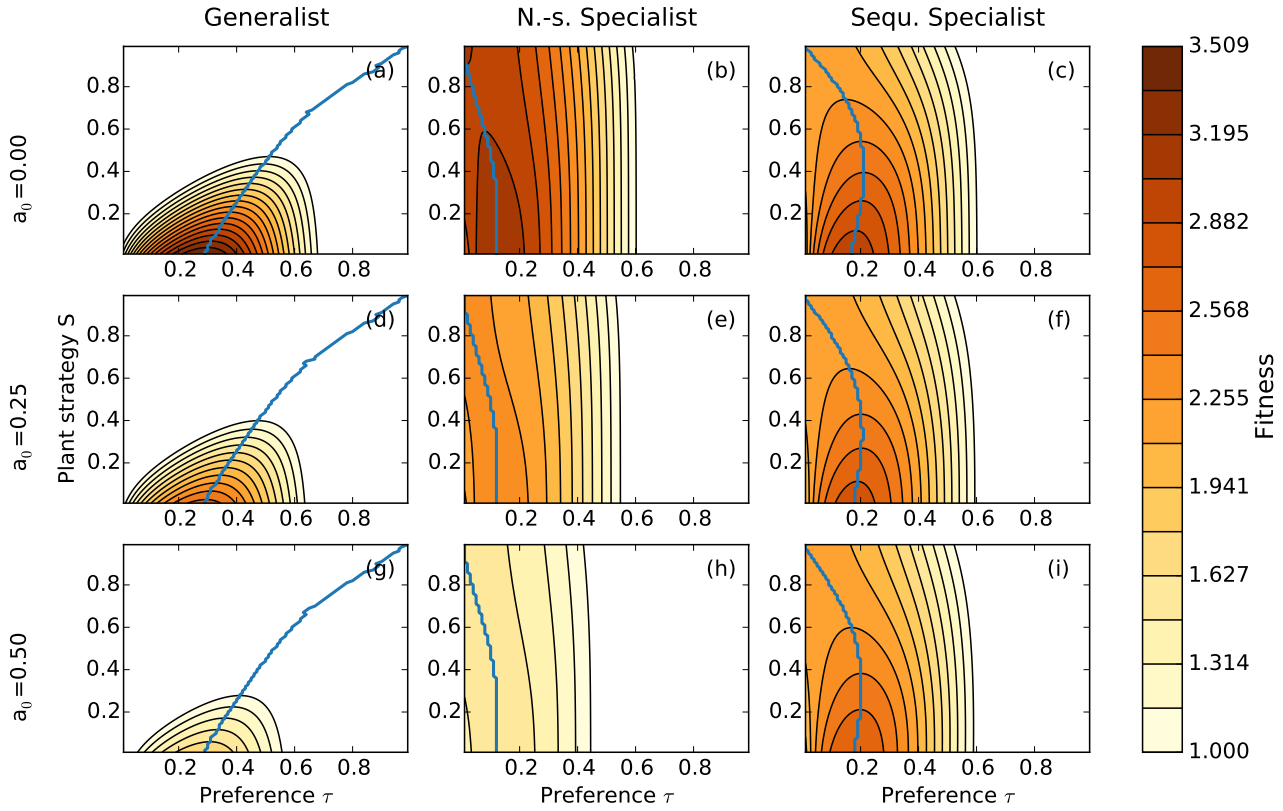

Figure 5.14.: Mean fitness (i.e. the mean number of offspring per herbivore individual reaching reproductive age; cp. Eq.(5.41)) of a population of generalists, sequestering, and non-sequestering specialists as a function of herbivore preference τ (cp. Eq.(5.9)) and the plant strategy parameter S (cp. Eq.(5.5)). The predator encounter rate a_0 (cp. Eq.(5.39)) increases from the top to the bottom row. The blue line indicates the optimal herbivore preference for a given plant strategy parameter S, i.e. the preference τ for which herbivore fitness is maximized.

vores that have considerable preference. However, the fitness of the generalist and the non-sequestering specialist considerably decrease with increasing predator encounter rate a_0 due to the lack of any mechanism to reduce the predation pressure. Hence, the plant may benefit from adapting to the sequestering specialist in this case.

However, herbivore preference is also an adaptable strategy. When the herbivores have time they will evolve to optimal preference which is the preference that maximizes herbivore fitness. This may be the case for constitutive defense mechanisms that vary with plant development and thus have a longer response time as inducible defenses (Karban et al., 1997). When the herbivores show optimal preference, the plant suffers from large defense level variability (i.e. low S) independently of the specialization strategy of its herbivores as indicated by the color change from lighter to darker color with decreasing S near the blue line.

These results are robust under changes of the efficiency of converting defense θ_S (s. Fig. G.6 in Appendix G; cp. Eq.(5.39)).

5.5.4 Impact of a correlation between the defense and the nutrient level of a leaf

Regularly, it is found that young leaves contain higher defense and nutrient levels than old leaves (Gutbrodt et al., 2012; Marsh et al., 2018; Cao et al., 2018; Travers-Martin and Müller, 2008). This implies that young leaves with a higher nutrient level are more valuable for the plant and thus better defended. In this section, we investigate the impact of this relationship between the nutrient and the defense level in a leaf (i.e. $l > 0$, (cp. Eq.(5.32))) on our results of the previous section, i.e. on the question whether defense level variability is *per se* beneficial for the plant. We choose $a_0 = 0.25$ for this investigation, but we checked that different predator encounter rates do not change the results qualitatively.

The resulting fitness functions $W_H(d)$ of a herbivore individual that feeds on a leaf with defense level d (and thus nutrient level $n(d)$) are shown in Fig. 5.13(a), (c), (e). When $l > 0$, the non-sequestering specialist benefits from feeding on medium-defended leaves as the performance increase due to the higher nutrient concentration in the leaves outweighs the performance loss caused by the higher defense level. The generalist, however, only performs better on weakly defended than on undefended leaves when the latter contain very low nutrient concentrations (i.e. $l = 1$). Otherwise, the generalist cannot benefit from the higher nutrient level in weakly and medium-defended leaves due to the high costs for dealing with plant defense. When $l > 0$, the fitness $W_H(d)$ of a generalist individual (and also the performance as $\theta = 0$; cp. Eq.(5.38)) is a concave downwards function of the plant defense level for which Jensen's inequality predicts that defense level variability is *per se* disadvantageous for the herbivore.

Fig. 5.15 shows the mean fitness of a herbivore population consisting of generalists, sequestering, and non-sequestering specialists in response to the plant strategy parameter S (cp. Eq.(5.5)) and herbivore preference τ (cp. Eq.(5.9)) for varying correlation parameter l (cp. Eq.(5.32)). The blue line indicates the optimal herbivore preference, i.e. the preference that maximizes herbivore fitness for a given plant strategy parameter S. Again, the white region shows the conditions under which herbivore fitness is below one which means that the herbivore population will go extinct.

When the defense and the nutrient level in a leaf are positively correlated, the generalist herbivore still benefits from high defense level variability. This is independent of its preference and the correlation parameter l, although the performance function $f(d)$ is a concave downwards function of the defense level d when $l > 0$. In this case, Jensen's inequality (and our results from Section 5.4) would predict that a herbivore with low preference suffers from large defense level variability. However, in the relevant range (i.e. around $d = 5$), the fitness (and thus the performance) function can still be approximated by a concave upwards function. Then, our findings here match those of Section 5.4.

Furthermore, the mean fitness considerably decreases with increasing correlation parameter l as the generalist suffers from the low nutrient concentration in weakly and undefended leaves (cp. Fig. 5.12 and 5.13). For $l = 1$, the generalist population can only reach fitness values that are larger than one in a tiny parameter range. Consequently, the plant *per se* benefits from increasing its nutrient level variability (for a given defense level variability, i.e. fixed S) when it is attacked by generalist herbivores.

In contrast to the case when all leaves contain the same nutrient level (i.e. $l = 0$), high defense (and thus nutrient) level variability (i.e. low S) is *per se* beneficial for a plant that is attacked by non-sequestering specialists independently of their preference when $l \geq 0.5$. This is indicated by the color change from darker to lighter color with decreasing plant strategy parameter S. As non-sequestering specialist individuals that feed on medium-defended leaves are the fittest (cp. Fig. 5.13(c), (e)), the population benefits from less defense level variability around the mean defense level. As a consequence, optimal herbivore preference decreases with increasing correlation parameter l as long as $S > 0$ because medium-defended leaves have the highest occurrence and the costs for

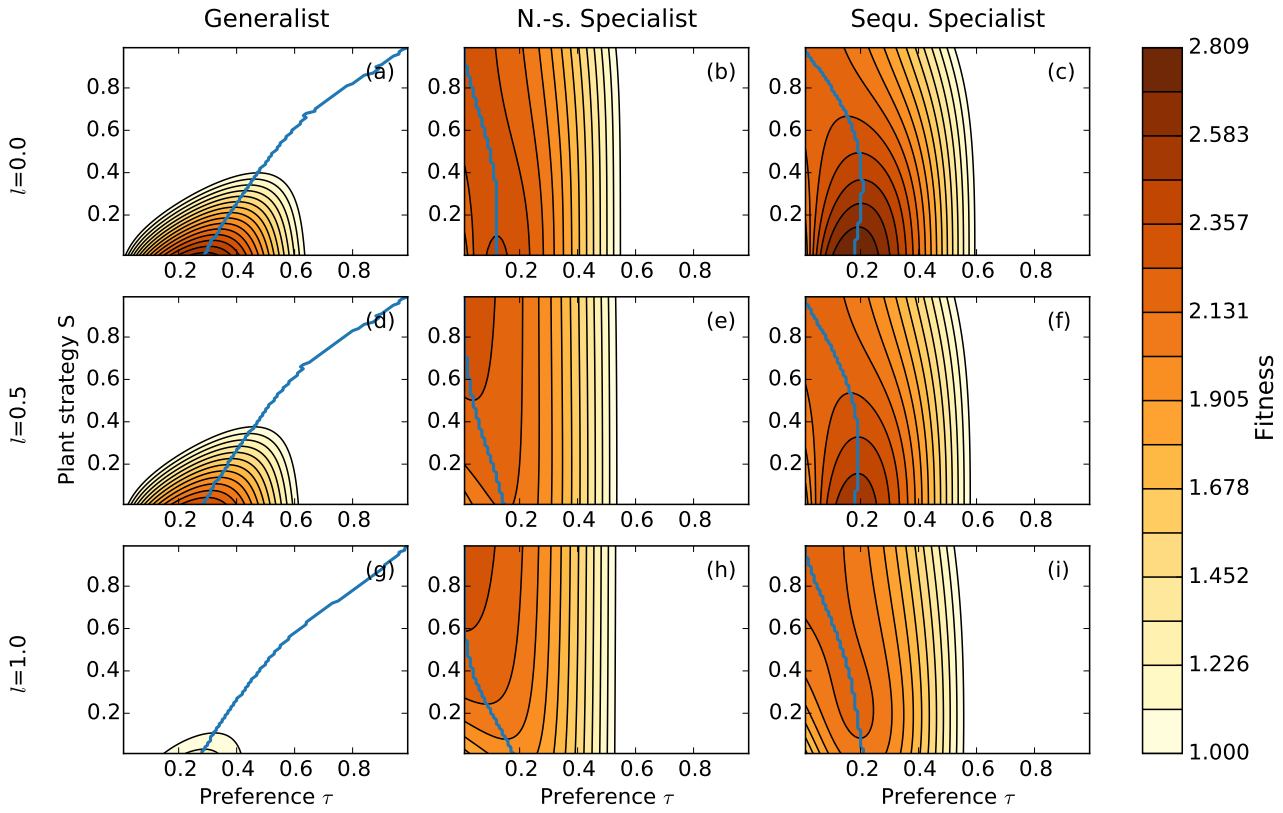

Figure 5.15.: Mean fitness (i.e. the mean number of offspring per herbivore individual reaching reproductive age; cp. Eq.(5.41)) of a population of generalists, sequestering, and non-sequestering specialists as a function of herbivore preference τ (cp. Eq.(5.9)) and the plant strategy parameter S (cp. Eq.(5.5)). The correlation parameter of the nutrient and defense level in the leaves l (and thus the nutrient level variability; cp. Eq.(5.32)) increases from top to bottom row. The blue line indicates the optimal herbivore preference for a given plant strategy parameter S, i.e. the preference τ for which herbivore fitness is maximized.

preference thus exceed its benefits. Indeed, this is in concert with our investigation of the nutrient performance function that looks like a concave downwards parabola from the previous Section 5.4.4.

Against a sequestering specialist, high defense level variability (i.e. low S) is still only *per se* beneficial for a plant when the herbivores have low preference. Otherwise, the plant suffers from high defense level variability. However, when herbivores have enough time to evolve to optimal herbivore preference, a plant, that is attacked by sequestering or non-sequestering specialists, benefits from high defense level variability (i.e. low S) as indicated by the color change from darker to lighter color with decreasing plant strategy parameter S near the blue line.

5.5.5 Impact of the effectiveness of plant defense against generalists

Plants have often evolved multiple defense substrates to deter herbivores that differ in their effectiveness against particular herbivores of a certain age (Dimarco et al., 2012; Elliger et al., 1976; Despres et al., 2007; Jeude and Fordyce, 2014; Blüthgen and Metzner, 2007). In the previous sections, we assumed that a generalist is very effectively deterred since it can only grow on a small defense level interval compared to the whole considered defense level range. In this section, we thus investigate the impact of a less effective plant defense against generalist herbivores. Consequently, we change the function for the proportional growth deficiency (cp. Eq.(5.37)) to

$$g(d, \nu) = \max\left[\left(2.5 - \frac{0.75}{\nu}\right)\left(\frac{d}{d_{\max}}\right)^{1/\nu}, 0\right], \tag{5.42}$$

with $\nu \geq 0.3$ and recalculate the mean fitness of a generalist population considering a cost factor $\nu = 1$. The resulting fitness functions $W_H(d)$ of a generalist herbivore individual feeding on a leaf with defense level d are shown in Fig. 5.16 for different (a) predator encounter rates a_0 (cp. Eq.(5.39)) and (b) correlation parameters l (cp. Eq.(5.32)). The generalist herbivore now reaches fitness values around one on medium-defended leaves.

Fig. 5.17 shows the mean fitness of a generalist herbivore population, that is less effectively deterred by plant defense, in response to the plant strategy parameter S (cp. Eq.(5.5)) and herbivore preference τ (cp. Eq.(5.9)). In the left panels, we increase the predator encounter rate a_0 and assume that all leaves contain the same nutrient concentration (i.e. $l = 0$) as in Section 5.5.3, in the right panels, we increase the correlation parameter l considering a predator encounter rate of $a_0 = 0.25$ as in Section 5.5.4.

As in the previous Sections 5.5.3 and 5.5.4, the generalist population benefits from large defense level variability independently of its preference τ, the predator encounter rate a_0, and the correlation parameter l, since its performance function (or fitness function $W_H(d)$) can still be approximated by a concave upwards function in the relevant range. The generalist population, however, reaches higher fitness values as in Section 5.5.3 and 5.5.4 under all considered conditions as being less effectively deterred by plant defense. For the same reason optimal preference deceases with increasing plant strategy parameter S (cp. Eq.(5.5)) when S is high in contrast to the findings of the previous Sections 5.5.3 and 5.5.4. As the generalist can grow on medium-defended leaves, it is not worth to take the high costs for finding weakly defended leaves when those are seldom as S is high.

Hence, our results of the previous sections are still valid when the herbivore is less effectively deterred by the plant defense.

5.5.6 Summary of major findings

Regarding our research questions (s. Section 5.5.2), we want to highlight some central findings of this study:

- Defense level variability is *per se* beneficial for a plant that is attacked by:
  1. Specialists that have low preference.
  2. Specialists that have optimal preference when nutrient level variability is high (i.e. large correlation parameter l).
  3. Non-sequestering specialists when nutrient level variability is high (i.e. correlation parameter $l = 0.5$ or higher) independent of their preference.
- Against generalist herbivores, large defense level variability is *per se* disadvantageous for a plant, however, the impact of the generalist on a plant crucially decreases with increasing nutrient level variability (i.e. large correlation parameter l).

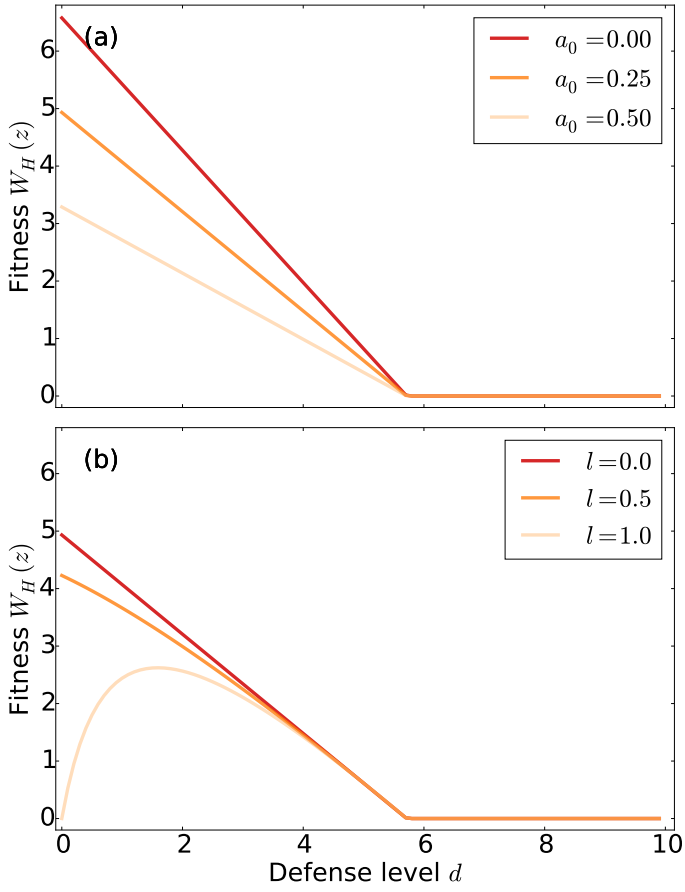

Figure 5.16.: Fitness $W_H(d)$ of a generalist individual feeding on a leaf with defense level d in dependency of (a) the predator encounter rate a_0 (cp. Eq.(5.39)) and (b) the correlation parameter l (cp. Eq.(5.32)). We chose $l = 0$ in (a) and $a_0 = 0.25$ in (b). The fitness functions $W_H(d)$ in (a) qualitatively correspond to the performance function.

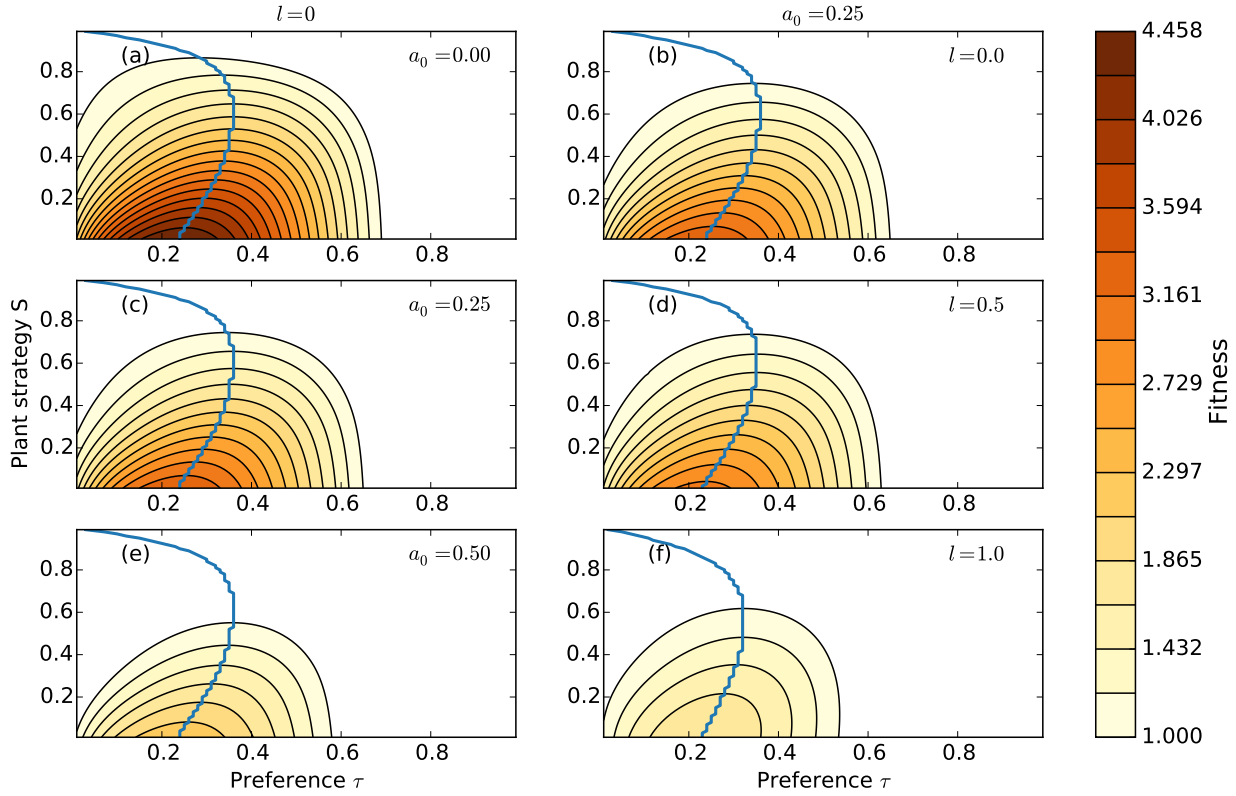

Figure 5.17.: Mean fitness (i.e. the mean number of offspring per herbivore individual reaching reproductive age; cp. Eq.(5.41)) of a generalist population that is less effectively deterred by the plant defense as a function of herbivore preference τ (cp. Eq.(5.9)) and the plant strategy parameter S (cp. Eq.(5.5)) for varying predator encounter rate a_0 (cp. Eq.(5.39)) ((a), (c), (e)) and correlation parameter l (s. Eq.(5.32)) ((b), (d), (f)). The blue line indicates the optimal herbivore preference for a given plant strategy parameter S, i.e. the preference τ for which herbivore fitness is maximized.

- The higher the predator encounter rate a_0, the larger is the impact of the sequestering specialist on the plant.

In the following section, we will discuss these results in detail.

5.5.7 Discussion

In this section, we investigated whether defense level variability is *per se* beneficial for a plant that is attacked by either generalists or sequestering or non-sequestering specialists. In particular, we focused on the impact of herbivore preference, the predator encounter rate, and a correlation between the defense and the nutrient level in a leaf on our findings. Note, that our results are valid for intra- and inter-individual defense level variability as well as for feeding and oviposition preference of the herbivores.

The form of the performance functions for the generalist, sequestering, and non-sequestering specialists, that we consider in this study when the leaves do not vary in their nutrient concentration, qualitatively agrees with the considerations in (Ali and Agrawal, 2012). This meta-study summarized published data concerning the plant response to specialist and generalist herbivores. Based on these data, Ali and Agrawal (2012) formulated predictions for the performance of generalist, sequestering, and non-sequestering specialist herbivores as a function of plant defense. The performance function for the sequestering specialist in (Ali and Agrawal, 2012) thereby qualitatively corresponds to our fitness function $W_H(d)$ of a sequestering specialist individual feeding on a leaf with defense level d, since we considered that the predation pressure does not affect the performance and thus the growth of herbivore individuals. Additionally, we could find empirical evidence for the assumptions that we made in order to find the expression for the performance functions (s. Section 5.5.1).

In contrast, Wetzel et al. (2016) found in their meta-study that the herbivore performance function should on average be linear which means that defense level variability has *per se* no influence on the plant-herbivore interaction. Furthermore, they found no correlation between the curvature of the performance function and the niche breadth of the herbivores. This may be caused by other factors that overlie this correlation. For instance, plants often have evolved several defense mechanisms that differ in their effectiveness against a specific herbivore (Dimarco et al., 2012; Elliger et al., 1976; Despres et al., 2007; Jeude and Fordyce, 2014; Blüthgen and Metzner, 2007). Hence, the form of the performance function may also depend on which defense mechanism is considered against which herbivore and additionally on the age of the herbivore (Dimarco et al., 2012; Elliger et al., 1976; Despres et al., 2007; Jeude and Fordyce, 2014; Blüthgen and Metzner, 2007). Furthermore, the data is often difficult to interpret such that different authors may extract different curvatures out of the same data. For instance, the larval growth in response to different levels of sunflower diterpene acids in (Elliger et al., 1976) has been cited as justification that the defense performance is a concave downwards function (Karban et al., 1997) or a complex function having both concave upwards and concave downwards regions (Ruel and Ayres, 1999).

We found that large defense level variability is *per se* disadvantageous for a plant that is attacked by generalist herbivores independent of their preference, the predator encounter rate, and additional nutrient level variability. With regard to our results of the previous Section 5.4 and the predictions of Jensen's inequality (Jensen, 1906; Bolnick et al., 2011), this was first surprising, as the performance function of the generalist is in general linear and even concave downwards when the nutrient variability is high (i.e. the correlation parameter l is large). However, in the relevant range (i.e. around the mean defense level), the performance function can be approximated by a concave upwards function, for which the predictions from the previous Section 5.4.4 correspond to our findings. Furthermore, we find that the impact of the generalist decreases with increasing predator encounter rate and nutrient level variability. Indeed, several plants have evolved mechanisms to produce indirect plant defense substances that attract enemies of the herbivores (Ali and Agrawal, 2012; Kahl et al., 2000).

Against specialists with low preference, large defense level variability is *per se* beneficial for a plant when all leaves contain the same nutrient concentration. However, specialists, that have high preference, benefit from large defense level variability. This is in concert with our results of the previous Section 5.4.4. In particular, the latter is true when the specialists have enough time to evolve to optimal preference.

We found that optimal preference is largest for the generalist followed by the sequestering specialist and the non-sequestering specialist. Hence, the larger the costs for dealing with plant defense, and thus the lower the defense level range where the herbivore can grow well, the higher is the optimal preference. Again, in Section 5.4.4 (and 5.4.5), we came to the same conclusion. Moreover, there are empirical evidence that supports these findings: For instance, Bellota et al. (2013) (and Jeude and Fordyce (2014)) found that herbivores have a stronger preference when the deterrent effectiveness of plant defense increases, although Jeude and Fordyce (2014) found no clear correlation. Additionally, van Leur et al. (2008) found that specialist herbivores have less preference for leaves on which they perform best than generalists.

When the defense level in a leaf is positively correlated with its nutrient level, a plant that is attacked by a non-sequestering specialist *per se* benefits from large defense level variability independently of herbivore preference. The reason is that the herbivore performs best on medium-defended leaves in this case. Indeed, we found the same result for the concave downwards parabola that has its maximum on the mean nutrient level in Section 5.4.4 as suggested by multiple studies (Zehnder and Hunter, 2009; Joern and Behmer, 1998; Fischer and Fiedler, 2000; Joern and Behmer, 1997; Boersma and Elser, 2006). Here, we showed that it suffices to perform slightly better on medium-defended leaves than on undefended ones and that such a performance function is for instance appropriate when considering the defense and the nutrient level of the leaves as variable traits. Indeed, Tao et al. (2014) argued that a concave downwards parabola is an appropriate performance function when leaves with high nutrient concentrations include a higher concentration of secondary metabolites.

Especially when changes in the plant strategy occur on longer time scales the herbivore population has enough time to develop optimal preference. This may be the case for constitutive defense mechanisms that vary with plant development and thus have a longer response time as inducible defenses (Karban et al., 1997). When the defense level in a leaf is positively correlated with its nutrient level, a plant that is attacked by sequestering (or non-sequestering) specialists with optimal preference benefits from large defense level variability. In this case, the plant mainly suffers herbivory by specialists as generalists are effectively deterred by the additional nutrient level variability. As it is regularly found that young leaves contain higher defense and nutrient levels than old leaves (Gutbrodt et al., 2012; Marsh et al., 2018; Cao et al., 2018) (although there are counterexamples (Quintero and Bowers, 2018)), this may be an explanation why on the one hand most orders of herbivorous insects are dominated by specialists (Schoonhoven et al., 2005; Bernays and Graham, 1988; Ali and Agrawal, 2012) and on the other hand why we observe such an enormous extent of defense level variability in nature (Poelman et al., 2008b; Lankau, 2007).

5.6 Conclusion

In this section, we briefly summarize the results of the previous Sections 5.4 and 5.5 in which we investigated the *per se* effect of defense and nutrient level variability.

In a nutshell, we found that one reason for the large nutrient and defense level variability observed in plant species may be its *per se* effect. We showed that the plant can reduce the fitness of herbivores by just altering the variability of these traits without changing the mean trait. It is reasonable that this does not includes higher costs for the plant in contrast to changing the mean trait level. Hence, trait variability may represent an important strategy for plants. We showed that it is crucial to consider herbivore preference to investigate the *per se* impact of trait variability. We furthermore found that such a beneficial *per se* effect of trait variability may occur when the nutrient and defense level of a leaf are positively correlated and when the herbivores have enough time to evolve to their optimal preference (which is especially relevant for constitutive plant defenses). Consequently, this may be an evolutionary stable strategy, i.e. a point in trait space where neither the herbivore nor the plant can increase their fitness (Maynard Smith, 1982; Drossel, 2001).

Hence, we showed that the *per se* effect may be a crucial factor to explain the large extent of trait variability in plants. Note, there may also be other reasons why trait variability is advantageous for a plant. For instance, Pearse et al. (2018) found that constraints on the response time of herbivores to physiologically track defensive variability of plants in time explains variability effects better than nonlinear averaging. In contrast, Stockhoff (1993) argued that the nonlinear relationship between food utilization efficiency and the nitrogen concentration may explain the reduced pupal mass of larvae of the gypsy moth that experience a diet of variable nitrogen concentrations compared to larvae that feed on the corresponding mean nitrogen concentration.

Hence, our investigations show that trait variability may be an important feature for plants. Indeed, this is similar to the findings of multiple empirical studies that the lack of crop genetic diversity crucially affects the ecosystem (Crutsinger et al., 2008; Tooker and Frank, 2012; Esquinas-Alcázar, 2005). For instance in the monocultures of modern agroecosystems, the lack of crop genetic diversity leads to more invasive species (Crutsinger et al., 2008), increased herbivory (Tooker and Frank, 2012; Peacock and Herrick, 2000), decreased plant fitness (Johnson et al., 2006a; Tooker and Frank, 2012), increased pest and pathogen pressure (Tooker and Frank, 2012; Esquinas-Alcázar, 2005), and higher vulnerability to abrupt climate changes (Esquinas-Alcázar, 2005). Preserving trait variability in plants should thus be an important goal of humanity.

6 Conclusion

In this chapter, we first summarize the results of all three parts of this thesis and then finally discuss our findings.

Summary

In this thesis, we investigated three mechanisms that enhance either species diversity (i.e. the number of coexisting species) or species abundance in the system under investigation, namely,

1. reducible defense in a predator-prey system (s. Section 3),
2. stochastic migration in a metacommunity even when migration events are very rare (s. Section 4), and
3. plant trait variability in a plant-herbivore system (s. Section 5).

In Section 3, we focused on reducible, reservoir-based defense. This means that the prey is able to defend against predator attacks by excreting a certain amount of secretion which is stored in a reservoir and biosynthetically restored with time. In order for an attack to be successfully repelled, the prey needs a certain amount of secretion and as long as it stores at least this amount, the prey is not consumable by the predator. For this system, we showed that reducible defense is beneficial for the prey when predator density is not too low and the costs for defense are not too large. When attacks happen in episodes separated by long recovery times, it is more favorable to have a large reservoir (and thus initial amount of secretion when the attack episode starts) than a fast refilling mechanism when both include considerable costs and the attacks are intense. On long time scales where we neglected this episodic nature of attacks, we found that reducible defense can enhance both predator and prey abundance since the prey benefits from the decreased consumption rate and the predator in turn profits from the increased prey density despite of the higher fraction of defended prey.

In Section 4, we investigated the impact of stochastic migration on a metacommunity consisting of several patches each containing a food web with multiple trophic levels. Although some studies showed that intermediate migration rates increase the biodiversity in metacommunities (Plitzko and Drossel, 2014) due to dynamical coexistence and the rescue effect, less was known about the limit of small migration rates. We found that species robustness (and thus diversity) increases when patches are coupled via a small migration rate compared to isolated patches. This even happens in the adiabatic limit, i.e. in the limit of very rare migration events where the system reaches an attractor between two migration events. Here, we further showed that a large spatial web can be static and homogeneous or heterogeneous in the long-term limit or can show ongoing-species replacement. As in the deterministic limit, we found that the diversity increases with increasing migration strength and that this increase is based on the rescue effect and dynamical coexistence (when migration events do not happen too infrequently). However, with stochastic migration, the diversity is higher than in the deterministic limit (when the migration strength is not too high) as both effects occur more frequently. Furthermore, we showed that both effects mostly happen for species of the second trophic level while species of the third trophic level suffer from low migration rates.

Finally, in Section 5, we focused on the impact of plant trait variability on a plant-herbivore system. Since plants typically vary in numerous traits, the question arises whether this trait variability is an evolutionary advantage for the plant. One hypothesis is that trait variability is *per se* beneficial for the plant as it reduces herbivory and thus increases the survival and the abundance of the plant based on Jensen's inequality. In this thesis we focused on this *per se* effect of the nutrient or/and the defense level variability in the leaves. We showed that trait variability is *per se* beneficial for the plant when the herbivore performance is a concave downwards function of the considered trait in the relevant trait range and the herbivores have low preference for instance due to high associated costs. When the performance function reaches its maximum on a medium-trait value, the plant benefits from a large trait variability independently of herbivore preference. Such a performance function is appropriate when considering the nutrient level as plant trait under the assumption that excess nutrients include considerable metabolic costs for removal or when the nutrient level in a leaf is positively correlated with its defense level. We further showed that the latter applies for a herbivore that can deal with a wide range of defense levels, i.e. for a specialist. However, when the

specialist has to take relatively high costs to deal with plant defense because of sequestering, the plant may only benefit from large defense and nutrient level variability when the sequestering specialist has optimal preference. Although defense (and nutrient level) variability is *per se* disadvantageous against generalist herbivores, specialist herbivores have a much larger impact on a plant when its leaves vary in both nutrient and defense level, such that in total the plant *per se* benefits from high defense and nutrient level variability.

Discussion

In this thesis, we broadened the knowledge about three features in antagonistic systems that have been found to impact the stability of ecological systems. We furthermore identified the conditions under which these features are beneficial for the species and thus conditions, under which these features may have evolved. The benefit of the species manifests for reducible defense and plant trait variability in an increase of their abundance, while migration via the rescue effect helps preserve species abundance on a spatial scale against perturbation that would lead to the extinction of the species.

Furthermore, the presence of these features also affects the ecosystem in which the species live, especially its stability. Migration can also increase the diversity in the metacommunity, i.e. the number of coexisting species, via dynamical coexistence. Indeed, several studies found evidence that diversity increases the stability of ecosystems through time (measured in decreased variability; cp. Chapter 1) (Loreau and de Mazancourt, 2013; McCann, 2000; McNaughton, 1985; Tilman, 1996; Tilman et al., 2006) and makes the ecosystem less prone to invasive species (i.e. higher resistance; cp. Chapter 1) (McCann, 2000) since all possible niches are occupied. A reason for the former may be that a decreased diversity leads to higher mean interaction strengths (McCann, 2000), which are known to decrease the stability of ecological systems (McCann et al., 1998). Furthermore, simple communities tend to larger oscillations of the populations whereby the species are more prone to extinction by demographic stochasticity (Williams, 2008; Elton, 1958). However, note that high diversity does not necessarily include population-level stability (McCann, 2000; Tilman, 1996).

Besides the increased prey abundance, reducible defense can simultaneously enhance predator abundance in a predator-prey system. Consequently, reducible defense can enhance the survival conditions of all species in the system as they are less prone to stochastic extinction (i.e. a higher resistance; cp. Chapter 1) (McCann et al., 1998) and thus also preserves biodiversity. Indeed, we showed a similar behavior in the plant-herbivore system, when the plant population is not large enough to be considered as constant over the simulation time. Hence, the herbivore benefits from the increased plant abundance despite of the lower mean performance. A reason for the comparable behavior may be that both reducible defense and trait variability promote heterogeneity on interindividual and intraspecific level, respectively.

However, both biodiversity and species abundance may not directly and unconditionally increase the stability of more complex ecosystems (McCann, 2000; Sankaran and McNaughton, 1999). For instance, biodiversity also enhances the efficiency of resource use, biomass production, and the recycling of essential nutrients (Cardinale et al., 2012; Loreau and de Mazancourt, 2013). Hence, the stability enhancing effect of biodiversity through time may be an indirect effect (Cardinale et al., 2012; Loreau and de Mazancourt, 2013). Additionally, an increase in species abundance can also destabilize ecosystems when becoming too large if this leads to oscillations with large amplitudes and thus to a higher probability of extinction through stochastic effects. For instance, an increasing carrying capacity can destabilize ecological systems (Pascual et al., 2006). Similarly, high availability of limiting resources, as for instance the resource in a consumer-resource model, is known to destabilize ecological systems (Rosenzweig, 1971; Vos et al., 2004a). This effect is known as “paradox of enrichment” (Rosenzweig, 1971) and may become important when considering reducible defense or plant trait variability in a more complex system. However, both features can also decrease the interaction strength between species and such mechanisms are known to decrease the amplitudes of these oscillations and thus enhance the stability of the ecological system (Vos et al., 2004a; Abrams and Walters, 1996). We conclude that the features, that we investigated in the course of this thesis, enhance the stability of the considered systems by increasing either biodiversity or species abundance (Loreau and de Mazancourt, 2013; McCann, 2000).

To conclude, this thesis contributes to a better understanding of the mechanisms underlying reducible defense, stochastic migration, and trait variability and their consequences on ecosystems. Indeed, based on these studies, we can hand out or rather underline some well known advice to preserve biodiversity and thus stability of our ecosystem: We should avoid (i) the intense fragmentation of ecosystems since this makes dynamical coexistence impossible and (ii) the large monocultures being common in modern agroecosystem (and thus low intraspecific trait variability) since this may *per se* decrease plant fitness.

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A Derivation of the Holling Type II functional response

Holling (1959a,b) assumed that the consumer has a delimited time T that it can use for

1. searching for food, T_s, and
2. handling resource individuals T_h, i.e. consuming and digesting it.

Denoting the number of resource individuals consumed per consumer in time T as Y and the time to handle on resource individuals as T_h, this means

$$T = T_s + T_h Y \,. \tag{A.1}$$

With the assumption that a consumer scans an area with a rate a, the number of resource individuals consumed per consumer Y is

$$Y = a T_s R \,, \tag{A.2}$$

where R describes the population density, i.e. the number of resource individuals per area. By including Eq.(A.2) in Eq.(A.1), the time available for searching can be expressed as

$$T_s = \frac{T}{1 + a T_h R} \,. \tag{A.3}$$

Now, Eq.(A.3) can be included in Eq.(A.2), such that we obtain the functional response (i.e. the number of resource individuals consumed per consumer and per time interval T)

$$F(R) = \frac{Y}{T} = \frac{aR}{1 + a T_h R} \,. \tag{A.4}$$

This is the Holling Type II functional response.

B Stochastic simulations with reducible defense

We performed individual-based stochastic simulations in order to test the quality of our expression to describe the fraction of defended prey $D(S)$ (cp. Eq.(3.13)) which was derived in Section 3.1.3. We describe the implementation and the results in detail in the following. This part of the study was performed by Andreas Brechtel except for Fig. B.2.

B.1 Methods

We implement the stochastic simulation using the Gillespie algorithm (Gillespie, 1977). We assume one predator individual that feeds on $n = 10$ prey individuals each having a secretion reservoir of size K_S. We further assume that initially all secretion reservoirs are completely filled, i.e. $S_i(t = 0) = K_S$, for all $i \in \Omega = \{1, \ldots, n\}$. The predator attacks the prey with a constant rate a. The time Δt until the next attack event on a randomly chosen prey individual i takes place is derived by using an exponential distribution with mean $\frac{1}{a}$. When a prey individual i is attacked that stores an amount of secretion of $S_i < e_S$, the prey is consumed by the predator and is replaced by a prey individual that stores the mean amount of secretion of the prey population right before the attack. Hence, we ensure that the number of prey individuals is kept constant. Furthermore, the predator needs time to deal with its food, such that the predator has no time for searching new prey during the handling time T_h. The amount of secretion stored by a prey individual k that survived an attack is reduced by the transferring constant e_S. Before executing an attack (i.e. at $t + \Delta t - \epsilon$ for a small positive value of ϵ), the amount of secretion stored by each prey individual $k \in \{1, \ldots, n\}$ is updated via

$$S_k(t + \Delta t - \epsilon) = K_S - [K_S - S_k(t)]e^{-\frac{p_S}{K_S}\Delta t}, \tag{B.1}$$

according to Eq.(3.10).

During simulation, we track the mean amount of secretion stored by the prey individuals and the fraction of defended prey. To ensure that all reservoir filling levels occur often enough to achieve good statistics, we run the simulation for a long time and repeat this multiple times. We furthermore divide the reservoir filling states into discrete bins to obtain smooth curves.

B.2 Results

We use $a = 30$, $p_S = 0.02$, $K_S = 1$ and $T_h = 0.6$ for the simulation, such that the ratios correspond to those in the main investigation (s. Tab. 3.1). The higher value for the discovery rate is necessary in order to gain good statistics over all possible reservoir filling states in an adequate time. The higher rate of attacks can be achieved by placing the prey individuals in a smaller arena.

Fig. B.1 shows the resulting fraction of defended prey as a function of the mean amount of secretion in the prey population for different transferring constants e_S (dashed lines). For comparison, we add the corresponding mean-field approximation (solid line) as defined in Eq.(3.13).

We choose different numbers of runs for each set of parameters to achieve comparable statistics since the number of time steps needed to reach equilibrium differ. We use in (a) 2000 runs with 10^4 steps each, in (b) 1000 runs with 10^4 steps each, in (c) 10^4 runs with 1000 steps each, and in (d) 10^5 runs with 100 steps each. In (a), we use twice as many data points as in (b), (c), and (d) (which were 10^7), because we doubled the number of bins for increased precision in (a) in order to resolve the steeper slope.

The mean-field approximation of the fraction of defended prey $D(S)$ differs most from the result of stochastic simulations when the transferring constant e_S is low (i.e. $e_S = 0.05$; s. Fig. B.1(a)) or high (i.e. $e_S = 0.6$; s. Fig. B.1(d)). In the latter case, the fraction of defended prey shows a stepped increase as a function of the mean amount of secretion per prey individual. However, the mean-field approximation and the stochastic simulation provide similar results for intermediate values of the transferring constant e_S (s. Fig. B.1(b), (c)).

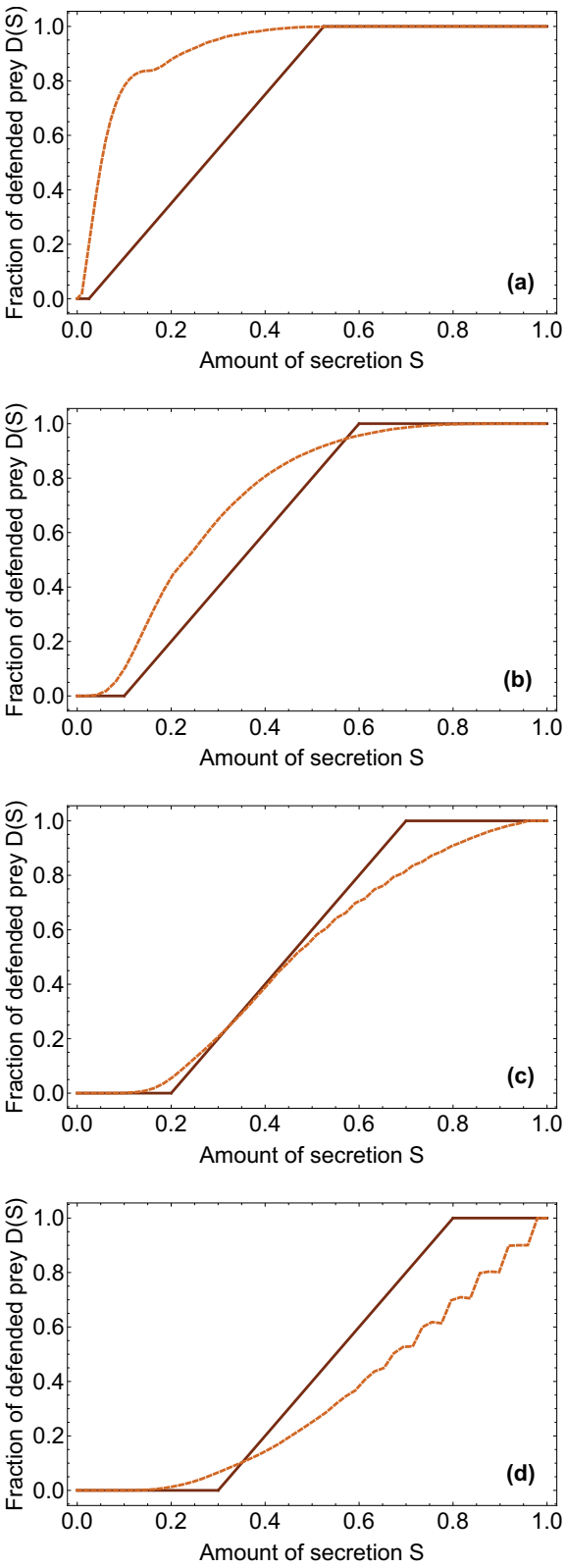

Figure B.1.: The fraction of defended prey plotted against the mean amount of secretion for a population of 10 prey individuals (dashed lines). The parameters of the stochastic simulations are: $a = 30$, $p_S = 0.02$, $K_S = 1$, $T_h = 0.6$. The transferring constant is in (a) $e_S = 0.05$, in (b) $e_S = 0.2$, in (c) $e_S = 0.4$, and in (d) $e_S = 0.6$. In (a) we used 100 bins in comparison to 50 bins in (b), (c), and (d). Between the bins, we used linear interpolation. For comparison, we add the corresponding mean-field approximation (solid line) as defined in Eq.(3.13).

Fig. B.2 shows the time evolution of the consumption rate per predator ((a), (d), (g), (j), (m)), the prey density ((b), (e), (h), (k), (n)), and the fraction of defended prey ((c), (f), (i), (l), (o)) in response to the regeneration rate p_S. In (d)-(f), (g)-(i), (j)-(l), and (m)-(o), we used the fraction of defended prey $D(S)$ from the stochastic simulation shown in Fig. B.1(a), (b), (c), and (d), respectively. For comparison, we show the results for the mean-field approximation of the fraction of defended prey $D(S)$ in Fig. B.2(a)-(c). The parameters that are not varied in a plot are set according to Tab. 3.1.

The results that we receive with the stochastic formulation of the fraction of defended prey do not qualitatively differ from those obtained with the mean-field approximation. The smaller the transferring constant e_S, the longer it takes the predator to disarm prey individuals and to thus make them consumable (s. Fig. B.2(d), (g), (j), (m) and (f), (i), (l), (o)). The time until all prey individuals are consumed decreases with increasing transferring constant e_S (s. Fig. B.2(b), (e), (h), (k), (n)).

Although the stepped increase of the fraction of defended prey as a function of the mean amount of secretion per prey individual received for a large transferring constant e_S (s. Fig. B.1(d)) transfers to the dynamics of prey consumption (s. Fig. B.2(m)-(o)), the general trends are the same as in the mean-field approximation. Especially the results obtained with the transferring constant $e_S = 0.2$ (s. Fig. B.2(g)-(i)), which we used in a large part of our study, differ even quantitatively only slightly from those received in the mean-field approximation (s. Fig. B.2(a)-(c)). We thus conclude that our expression for the fraction of defended prey $D(S)$ (s. Eq.(3.13)) is appropriate.

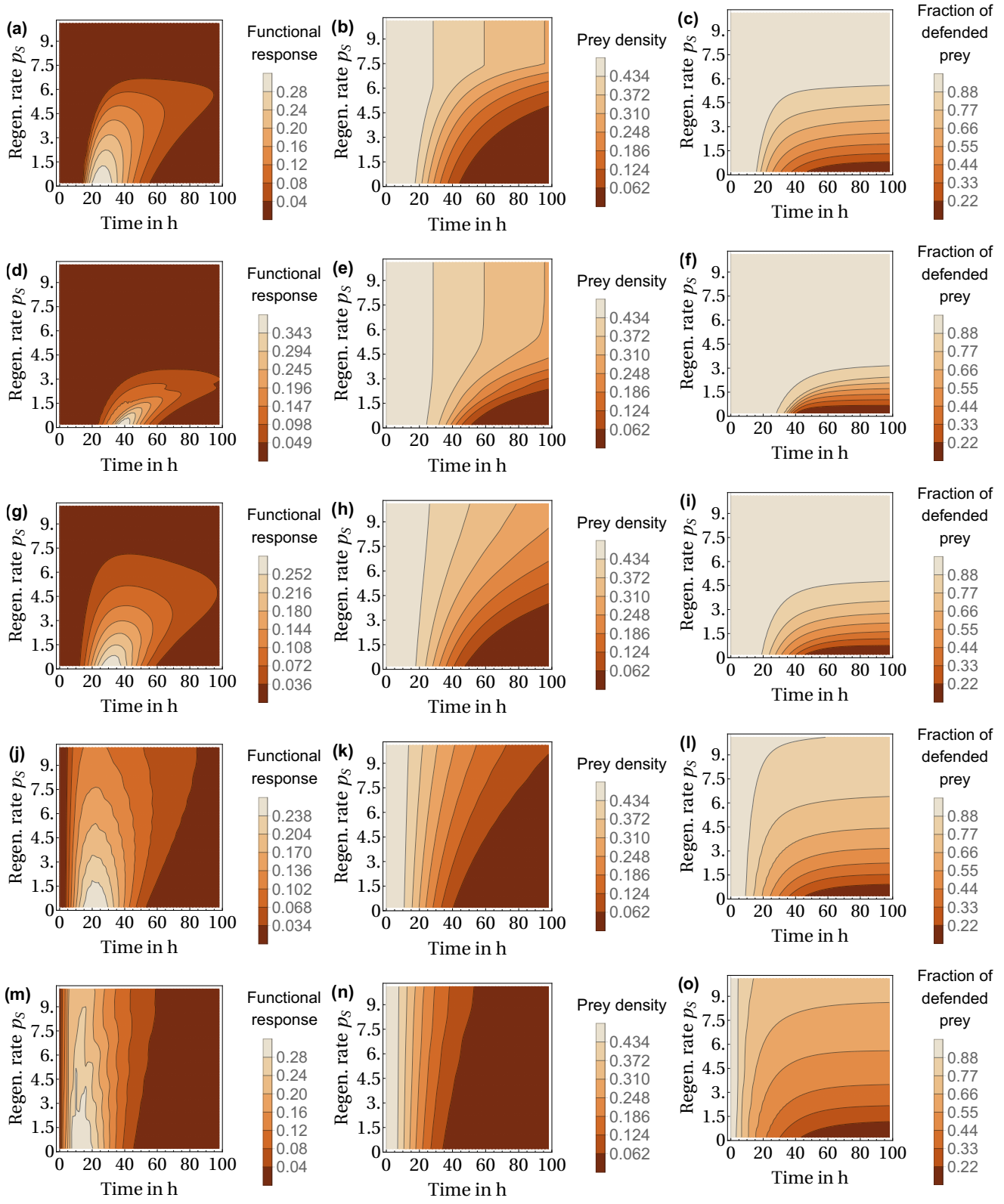

Figure B.2.: The dynamics of prey consumption as a function of time and the regeneration rate p_S using the four functional forms to describe the fraction of defended prey $D(S)$ shown in Fig. B.1 ($e_S = 0.05$: (d)-(f); $e_S = 0.2$: (g)-(i); $e_S = 0.4$: (j)-(l); $e_S = 0.6$: (m)-(o)). For comparison we added the results for the version used in the main part of this thesis ((a)-(c)). The different color shades indicate the prey consumption rate ((a), (d), (g), (j), (m)), prey density ((b), (e), (h), (k), (n)), and the fraction of defended prey ((c), (f), (i), (l), (o)). The parameters that are not varied in a plot are set to the values given in Tab. 3.1.

C Trade-off between the reservoir size and the growth rate on the long time scales

Similar to the investigation of reducible defense in the long-term limit (s. Fig. 3.3), we analyze the trade-off between investing in growth and defense via the reservoir size K_S on long time scales.

Fig. C.1 shows (a) the prey density, (b) the predator density, and (c) the fraction of defended prey in response to the reservoir size K_S and its cost factor ϑ. The white region indicates where the predator goes extinct.

As expected, we find the qualitative same behavior as in Fig. 3.3, where we varied the investment in defense via the regeneration rate p_S: The prey benefits from defense when the associated costs are not too high. When the costs are low, the predator also benefits from defense as the increase of the consumption rate due to the higher prey density outweighs its decrease caused by the higher fraction of defended prey. The prey can even benefit from increasing costs for defense since the decreased consumption rate due to the decreased predator density outweighs this cost increase (i.e. for $K_S = 75$ and an increasing cost factor $\vartheta > 0.0015$). This is concert with our results in Section 3.6.

Furthermore, both predator and prey first suffer from a small, but increasing reservoir size K_S for a high and fixed cost factor ϑ as illustrated by the color change from lighter to darker color with increasing K_S. This is the case as the costs for defense are higher than the benefit which leads to the decrease in prey density and as a consequence to the decrease in predator density. The prey density then increases for further increasing reservoir size K_S. In contrast to the findings of Fig. 3.3, the predator density also increases and then decreases again with further increasing investment in defense via the reservoir size K_S. This indicates that investment in defense becomes beneficial for the prey due to the decrease in predator density, although this decrease is non-monotonical.

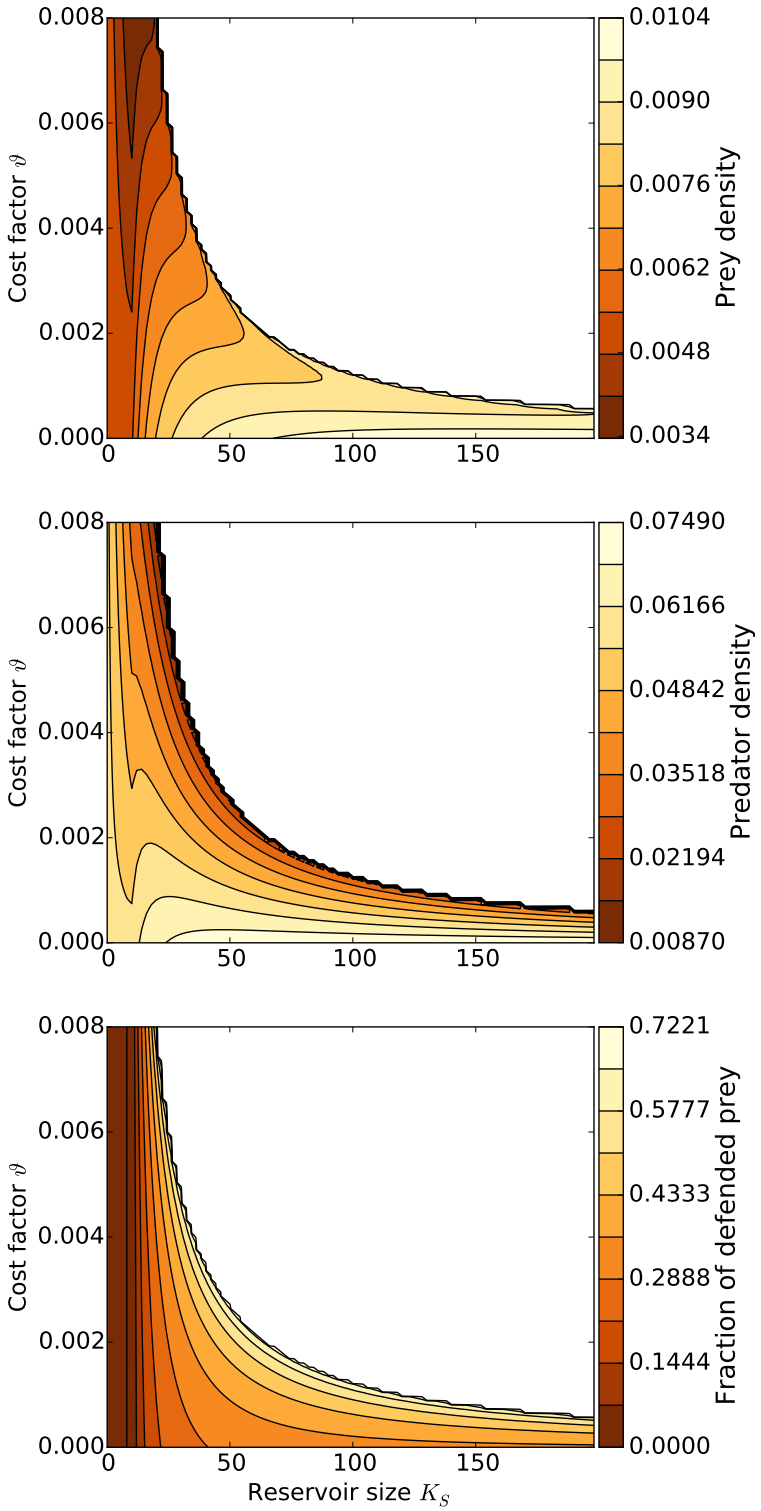

Figure C.1.: (a) Prey density, (b) predator density, and (c) the fraction of defended prey displayed in color code as a function of reservoir size K_S and its cost factor ϑ. The white region indicates where the predator goes extinct.

D Stochastic migration

We use the Gillespie algorithm (Gillespie, 1976, 1977) for the implementation of stochastic migration, which we explain in detail in this section.

D.1 Implementation via Gillespie algorithm

For stochastic migration, we follow the following plan of procedures:

1. Determinate the next migration event. This includes the choice of the directed link, the migrating species as well as the time of the next migration event (the exact calculations are shown below in Eq.(D.5)).
2. Calculate local population dynamics until the time of the next migration event is reached.
3. When the time of the next migration event is reached shift the migrating biomass unit B_{migr} to the determined patch.
4. Go back to step one until the set simulation time has ended.

As in Chapter 4, we denote the number of species as S and the number of patches as Y. The patch μ for emigration is chosen proportionally to the amount of biomass that the patch contains, i.e. $B^\mu = \sum_{i=1}^{S} B_i^\mu$, and the number of links that the patch has which we denote as h^μ. The patch μ is chosen for an emigration event with a rate

$$a^\mu = dh^\mu \frac{B^\mu}{B_{\text{migr}}}, \tag{D.1}$$

with migration strength d (cp. Eq.(4.7)) and the migrating biomass unit B_{migr}. The patch of immigration is then chosen randomly among all patches that are connected to the patch of emigration, i.e. with probability $\frac{1}{h^\mu}$. Hence, the probability that patch μ is chosen for immigration depends on the probability that a connected patch ν is chosen for emigration, i.e.

$$e^\mu = \sum_{\nu \in P_\mu} \frac{a^\nu}{h^\nu a_0}, \tag{D.2}$$

where P_μ is the set of patches linked to the patch μ and

$$a_0 = \sum_{\mu=1}^{Y} a^\mu \overset{(D.1)}{=} \sum_{\mu=1}^{Y} dh^\mu \frac{B^\mu}{B_{\text{migr}}}. \tag{D.3}$$

Note, that $\sum_\mu e^\mu = 1$. The selection probability for a species to migrate is chosen proportionally to its biomass in the patch, i.e.

$$s_i^\mu = \frac{B_i^\mu}{B^\mu}. \tag{D.4}$$

In practice, the time of the next migration event τ, as well as the patch μ for emigration and the species ξ involved in the migration event are calculated via the random numbers r_1, r_2, and r_3, that are chosen uniformly from an interval $(0, 1)$, as follows

$$\tau = \frac{1}{a_0}\ln\left(\frac{1}{r_1}\right)$$
$$\sum_{i=1}^{\mu-1} a^i < r_2 a_0 \leqslant \sum_{i=1}^{\mu} a^i \tag{D.5}$$
$$\sum_{i=1}^{\xi-1} s_i^u < r_3 s_0 \leqslant \sum_{i=1}^{\xi} s_i^u\,,$$

with $s_0 = \sum_{i=1}^{S} s_i$.

Indeed, with this choice of parameter values, we end up with the same equation for migration as in the deterministic limit (s. Eq.(4.7)). We will show this in the following.

Let us consider Z migration events in the whole simulation time T. In each migration event a fixed migrating biomass unit B_{migr} migrates. Hence, the amount of migrating biomass per time step is $\frac{ZB_{\text{migr}}}{T}$. As the number of migration events is $Z = \frac{T}{\bar{\tau}}$ with the mean time between two migration events $\bar{\tau}$, the amount of migrating biomass per time step is

$$M = \frac{B_{\text{migr}}}{\bar{\tau}}\,. \tag{D.6}$$

In order to describe the migrating biomass per species, time step, and patch as in the deterministic case in Eq.(4.7), we need to include the probability that the patch u is chosen for immigration or emigration as well as the probability that species i migrates as defined above (i.e. Eq.(D.1), (D.2), and (D.4)). We thus find

$$M_i^u(\vec{B}) = \frac{B_{\text{migr}}}{\bar{\tau}} \sum_{v\in P_u} \frac{a^v}{a_0 h^v} s_i^v - \frac{B_{\text{migr}}}{\bar{\tau}} \frac{a^u}{a_0} s_i^u\,. \tag{D.7}$$

Using the time between two migration events τ (s. Eq.(D.5)), we find for its mean

$$\bar{\tau} = \frac{1}{a_0} \overset{(D.3)}{=} \left(d \sum_{i,u} \frac{B_i^u}{B_{\text{migr}}} h^u \right)^{-1}. \tag{D.8}$$

In Section D.2, we show the first step in detail. By including this expression (D.8) in Eq.(D.7) (in form of $\bar{\tau} = \frac{1}{a_0}$), we find

$$\begin{aligned}
M_i^u(\vec{B}) &= B_{\text{migr}} \sum_{v\in P_u} \frac{a^v}{h^v} s_i^v - B_{\text{migr}} a^u s_i^u \\
&\overset{(D.1)}{=} d \sum_{v\in P_u} \left(\sum_i B_i^v \right) s_i^v - d \left(\sum_i h^u B_i^u \right) s_i^u \\
&\overset{(D.4)}{=} d \sum_{v\in P_u} \left(\sum_i B_i^v \right) \frac{B_i^v}{\sum_i B_i^v} - d h^u \left(\sum_i B_i^u \right) \frac{B_i^u}{\sum_i B_i^u} \\
&= d \left(\sum_{v\in P_u} B_i^v - h^u B_i^u \right) = d \sum_{v\in P_u} \left(B_i^v - B_i^u \right).
\end{aligned} \tag{D.9}$$

Hence, considering a large number of individuals that migrate we obtain the same migration term as in the deterministic case (cp. Eq.(4.7)).

D.2 Mean time between two migration events

Here, we concentrate on the calculations of the mean time between two migration events, i.e. $\bar{\tau} = \frac{1}{a_0}$. The time between two migration events is $\tau = \frac{1}{a_0}\ln\left(\frac{1}{r_1}\right)$ with a random number r_1 which is uniformly distributed in $r_1 \in (0,1)$. We will thus show that the expected value $E\left(\ln\left(\frac{1}{r_1}\right)\right) = 1$.
In our case, the expected value can be calculated as follows:

$$E(g(X)) := \int g(z) f_X(z)\,\mathrm{d}z \tag{D.10}$$

with $f_X(z) = \begin{cases} 1 & 0 < z < 1 \\ 0 & \text{otherwise} \end{cases}$ and $g(z) = \ln\left(\frac{1}{z}\right)$. Hence, we find

$$\begin{aligned} \lim_{c\to 0}\int_c^1 \ln\left(\frac{1}{z}\right)\mathrm{d}z &= -\lim_{c\to 0}\int_c^1 \ln(z)\mathrm{d}z \\ &= -\lim_{c\to 0}[z\ln(z) - z]_c^1 \\ &= -\lim_{c\to 0}(-1 - (c\ln(c) - c)) = 1. \end{aligned} \tag{D.11}$$

Thus, we have shown that $\bar{\tau} = \frac{1}{a_0}$, when the time between two migration events is $\tau = \frac{1}{a_0}\ln\left(\frac{1}{r_1}\right)$ with a random number $r_1 \in (0,1)$.

E Generation based modeling

In Chapter 5, we describe the population dynamics on generation basis, since the investigated main features, i.e. plant trait variability and herbivore preference, usually cannot be adapted on the typical time scale of feeding interactions. We rather assume that changes of these features are based on plastic responses to the environment or changes in the genotype of the species. These features can hence be seen as evolutionary strategies. The basic population dynamics equation shown in Eq.(2.1) can easily be transformed to a generation-based equation, which we will show in the following.

In order to distill the *per se* effect of plant trait variability on the herbivore population, we focus on the herbivore population dynamics. Hence, we assume that plant population is large enough to be considered as constant over the time scales covered in our model. Consequently, the herbivore population is small compared to the plant population, such that we assume that intraspecific competition is negligible. Starting with the predator dynamics of our basic consumer-resource model defined in Eq.(2.1), we find by neglecting intraspecific competition and by integrating over the time of one generation $[t_1, t_2]$

$$\begin{aligned}
\frac{\mathrm{d}C}{\mathrm{d}t} &= (\lambda F(R) - \alpha_C)\, C \\
\int_{C(t_1)}^{C(t_2)} \frac{\mathrm{d}C}{C} &= \int_{t_1}^{t_2} (\lambda F(R) - \alpha_C)\, \mathrm{d}t \\
\frac{C(t_2)}{C(t_1)} &= \exp\left((\lambda F(R) - \alpha_C)(t_2 - t_1)\right) \\
C(\tau+1) &= C(\tau) \exp\left(\lambda F(R) - \alpha_C\right) \\
C(\tau+1) &= C(\tau)\overline{W}
\end{aligned} \tag{E.1}$$

with the mean population fitness

$$\begin{aligned}
\overline{W} &= \exp\left(\lambda F(R) - \alpha_H\right) \\
&= \Lambda A.
\end{aligned} \tag{E.2}$$

Here, Λ describes the feeding interaction and A the metabolic loss per predator during the time of one generation. We are, however, interested in intraspecific variability in a resource trait, such that we choose another way to describe the mean fitness. We introduce this model in Section 5.3.

F Proof Jensen's inequality

In this section, we proof Jensen's inequality, which states that

$$f\left(\sum_{i=0}^{n}\lambda_i z_i\right) \leq \sum_{i=0}^{n}\lambda_i f(z_i) \tag{F.1}$$

with $\sum_{i=0}^{n}\lambda_i = 1$, $n \in \mathbb{N}$, when $f(z)$ is a concave upwards function. A function is concave upwards when

$$f(tx+(1-t)y) \leq tf(x)+(1-t)f(y), \tag{F.2}$$

for all $t \in (0,1)$. We use induction to proof this theorem:

- **Base case:** Be $n = 0$; then $\lambda_0 = 1$ and we find that

$$f(\lambda_0 z_0) = f(z_0) = \lambda_0 f(z_0). \tag{F.3}$$

- **Induction assumption:** We assume that Eq.(F.1) is true for an $n \in \mathbb{N}$.
- **Induction step:** Let's consider $n+1$, i.e

$$\sum_{i=0}^{n+1}\lambda_i = 1$$
$$\lambda_{n+1} = 1-\sum_{i=0}^{n}\lambda_i. \tag{F.4}$$

We find

$$\begin{aligned}
f\left(\sum_{i=0}^{n+1}\lambda_i z_i\right) &= f\left(\sum_{i=0}^{n}\lambda_i z_i + \lambda_{n+1}z_{n+1}\right)\\
&= f\left((1-\lambda_{n+1})\underbrace{\sum_{i=0}^{n}\frac{\lambda_i z_i}{(1-\lambda_{n+1})}}_{z'} + \lambda_{n+1}z_{n+1}\right)\\
&= f\left((1-\lambda_{n+1})z' + \lambda_{n+1}z_{n+1}\right)\\
&\overset{(F.2)}{\leq} (1-\lambda_{n+1})f(z') + \lambda_{n+1}f(z_{n+1})\\
&= (1-\lambda_{n+1})f\left(\sum_{i=0}^{n}\underbrace{\frac{\lambda_i}{(1-\lambda_{n+1})}}_{\lambda_i'} z_i\right) + \lambda_{n+1}f(z_{n+1})\\
&= (1-\lambda_{n+1})f\left(\sum_{i=0}^{n}\lambda_i' z_i\right) + \lambda_{n+1}f(z_{n+1}).
\end{aligned}$$

Here, we use the induction assumption and find

$$
\begin{aligned}
f\left(\sum_{i=0}^{n+1}\lambda_i z_i\right) &\leq (1-\lambda_{n+1})\sum_{i=0}^{n}\lambda_i' f\left(z_i\right) + \lambda_{n+1} f\left(z_{n+1}\right) \\
&= \sum_{i=0}^{n}\lambda_i f\left(z_i\right) + \lambda_{n+1} f\left(z_{n+1}\right) \\
&= \sum_{i=0}^{n+1}\lambda_i f\left(z_i\right) . \qquad \text{(F.5)}
\end{aligned}
$$

Hence, we showed the validity of Eq.(F.1) for all $n \in \mathbb{N}$.

G Robustness tests in the plant-herbivore model

In this chapter, we test the robustness of the results of Chapter 5 in response to changes of parameters and considered functions in the model.

G.1 Proportional growth deficiency

First, we test the robustness of our results under changes in the functional form of the proportional growth deficiency $g(d, \nu)$ (cp. Eq.(5.37)). Another function that satisfies the assumptions in Section 5.5.1 with an appropriate choice of parameter values, is

$$g(d, \nu) = \max\left[1 - \frac{\nu^3}{8500} d \exp\left(d/\nu\right), 0\right]. \tag{G.1}$$

Fig. G.1 shows the resulting performance functions and the fitness $W_H(d)$ of a herbivore individual feeding on a leaf with defense level d in dependency of the predator encounter rate a_0 (cp. Eq.(5.39)) and the correlation parameter l (cp. Eq.(5.32)). We use the parameter values shown in Tab. G.1 for this investigation. The functions have a similar form as in Fig. 5.13.

Table G.1.: Parameter values used for distinguishing the different herbivore strategies using the proportional growth deficiency $g(d, \nu)$ of Eq.(G.1).

	Generalist	**Non-seq. specialist**	**Seq. specialist**
Cost parameter ν	12.5	2.5	0.67
Generalist benefit factor γ	2	1	1
Efficiency of converting defense θ_S	0	0	10

Fig. G.2 shows the mean fitness of a herbivore population consisting of generalists, sequestering, and non-sequestering specialists in dependency of the plant strategy parameter S (cp. Eq.(5.5)) and herbivore preference τ (cp. Eq.(5.9)) for different correlation parameter l. We used a predator encounter rate of $a_0 = 0.25$ for this investigation. The blue line indicates the optimal herbivore preference, i.e. the preference that maximizes herbivore fitness for a given plant strategy parameter S. Again, the white region shows the conditions under which herbivore fitness is below one which means that the herbivore population goes extinct with proceeding time.

The fitness landscapes do not qualitatively differ from those in Fig. 5.15. As the sequestering specialist can deal worse with plant defense with our choice of parameter values than in Section 5.5, the fitness values change in a broader range. Hence, the fitness increase with decreasing plant strategy parameter S when approximately $S > 0.9$ (as herbivores show no preference and have a concave downwards performance function) is more clearly visible. We conclude that the results are robust under changes of the functional form of the proportional growth deficiency $g(d, \nu)$ under the assumptions proposed in Section 5.5.1.

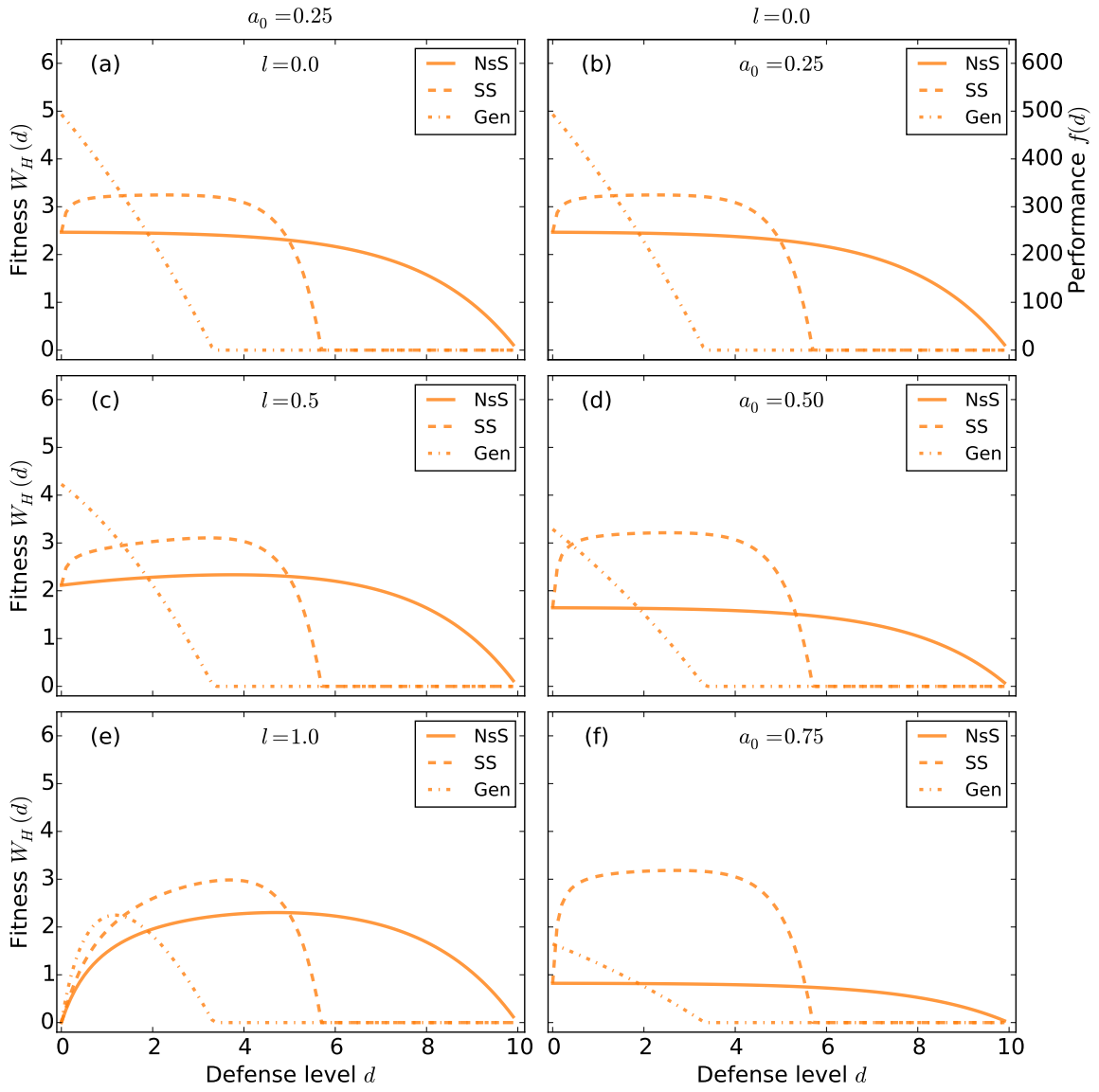

Figure G.1.: Fitness $W_H(d)$ (cp. Eq.(5.38)) of a herbivore individual that feeds on a leaf with defense level d using the proportional growth deficiency $g(d, v)$ of Eq.(G.1) under the assumption of different predator encounter rates a_0 (cp. Eq.(5.39)) and correlation parameters l (cp. Eq.(5.32)).

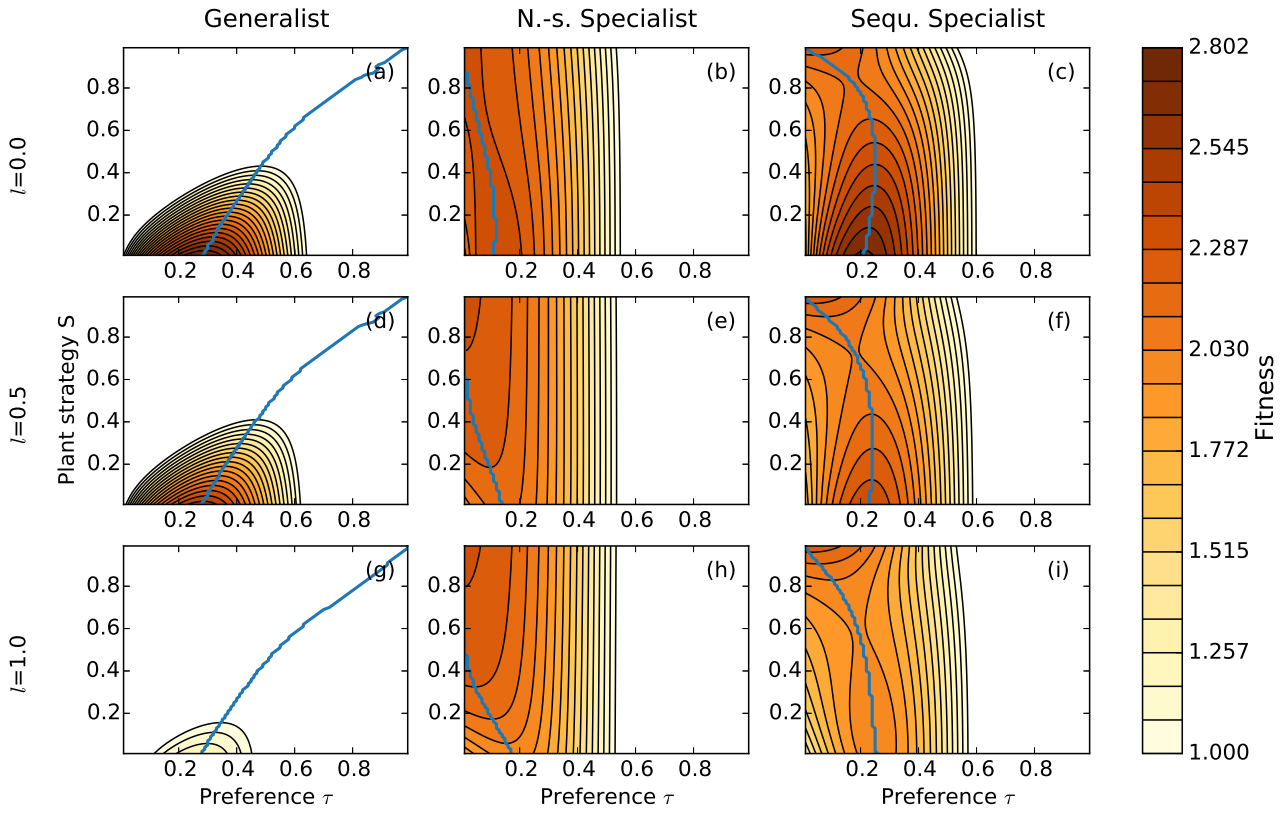

Figure G.2.: Mean fitness (i.e. the mean number of offspring per herbivore individual reaching reproductive age; cp. Eq.(5.41)) of a population of generalists, sequestering, and non-sequestering specialists as a function of herbivore preference τ (cp. Eq.(5.9)) and the plant strategy parameter S (cp. Eq.(5.5)). We used the proportional growth deficiency $g(d, v)$ of Eq.(G.1) for this figure. The correlation parameter of the nutrient and defense level in the leaves l (and thus the nutrient level variability; cp. Eq.(5.32)) increases from top to bottom row. The blue line indicates the optimal herbivore preference for a given plant strategy parameter S, i.e. the preference τ for which herbivore fitness is maximized.

G.2 Probability to be consumed by a predator

Here, we test the robustness of our results under changes of the functional form of the probability to be consumed by a predator $a(d)$ (cp. Eq.(5.39)). Hence, we focus on sequestering specialists in this section. Other functions that satisfy the assumptions in Section 5.5.1 with an appropriate choice of the parameter values, are

$$a_1(d) = a_0 e^{-0.5\theta d}, \tag{G.2}$$

$$a_2(d) = \frac{a_0}{1+\theta d^3}, \tag{G.3}$$

and are shown in Fig. G.3. We denote the functional form that we used in the main part of this thesis as $a_0(d)$ in this section (cp. Eq.(5.39)). For the efficiency of converting plant defense, we use $\theta_S = 10$ for all functional forms of the probability to be consumed by a predator $a(d)$. We analyze the impact of varying values of the efficiency of converting plant defense θ_S in Section G.3.

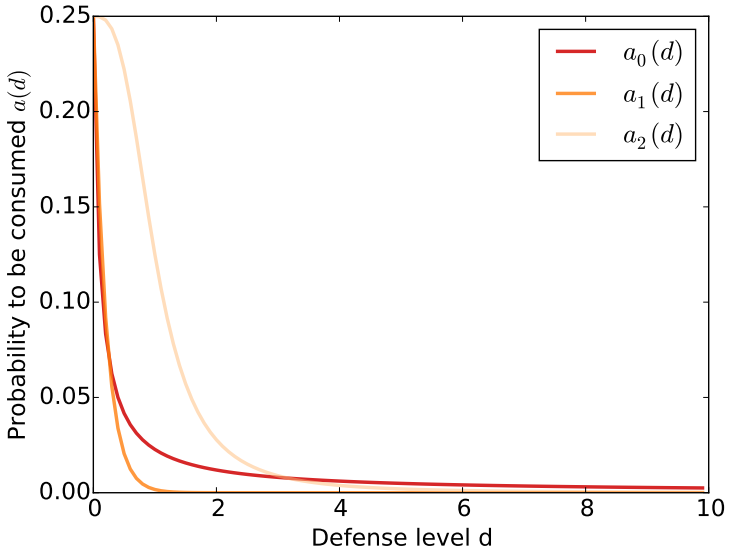

Figure G.3.: Different functional forms of the probability to be consumed by a predator $a(d)$ for $a_0 = 0.25$: $a_0(d) = \frac{1}{1+\theta d}$ (cp. Eq.(5.39)), $a_1(d) = e^{-0.5\theta d}$, and $a_2(d) = \frac{1}{1+\theta d^3}$. We used $\theta_S = 10$ for all considered functions.

The different functional forms of the probability to be consumed by a predator $a(d)$ only have a small impact on the fitness $W_H(d)$ (cp. Eq.(5.38)) of a sequestering specialist individual that feeds on a leaf with defense level d (s. Fig. G.4).

Fig. G.5 shows the mean fitness of a herbivore population consisting of sequestering specialists in dependency of the plant strategy parameter S (cp. Eq.(5.5)) and herbivore preference τ (cp. Eq.(5.9)) for these different functional forms of the probability to be consumed by a predator $a(d)$. The predator encounter rate a_0 increases from the left to the right panels. For this investigation, we assume that all leaves contain the same nutrient level, i.e. $l = 0$ (cp. Eq.(5.32)). The blue line indicates the optimal herbivore preference, i.e. the preference that maximizes herbivore fitness for a given plant strategy parameter S. The white region shows the conditions under which herbivore fitness is below one which means that the herbivore population goes extinct with proceeding time.

The fitness landscapes do not differ qualitatively. The predator encounter rate a_0 for which a herbivore population that feeds on a plant with $S > 0$ is fitter than one feeding on a plant with $S = 0$ differ slightly between the different functional forms of the probability to be consumed by a predator $a(d)$.

We conclude that the results are robust under changes of the functional form of the probability to be consumed by a predator $a(d)$.

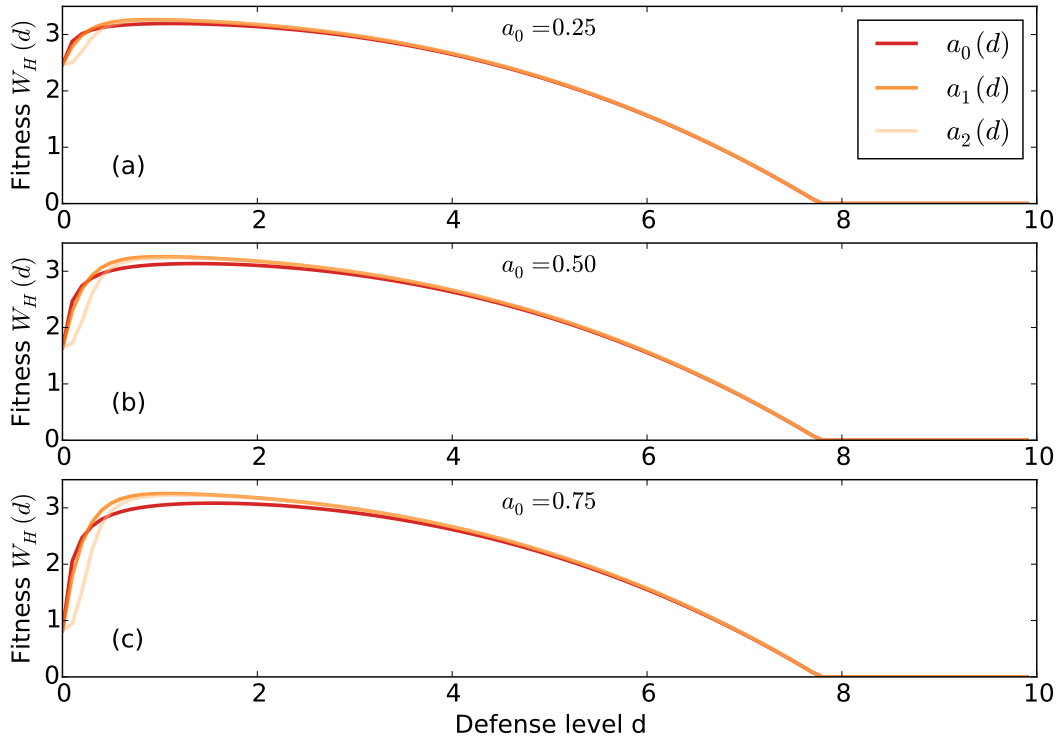

Figure G.4.: Fitness $W_H(d)$ (cp. Eq.(5.38)) of a sequestering specialist individual that feeds on a leaf with defense level d assuming different functional forms of the probability to be consumed by a predator $a(d)$ (cp. Fig. (G.3)). From up to down, we increase the predator encounter rate a_0.

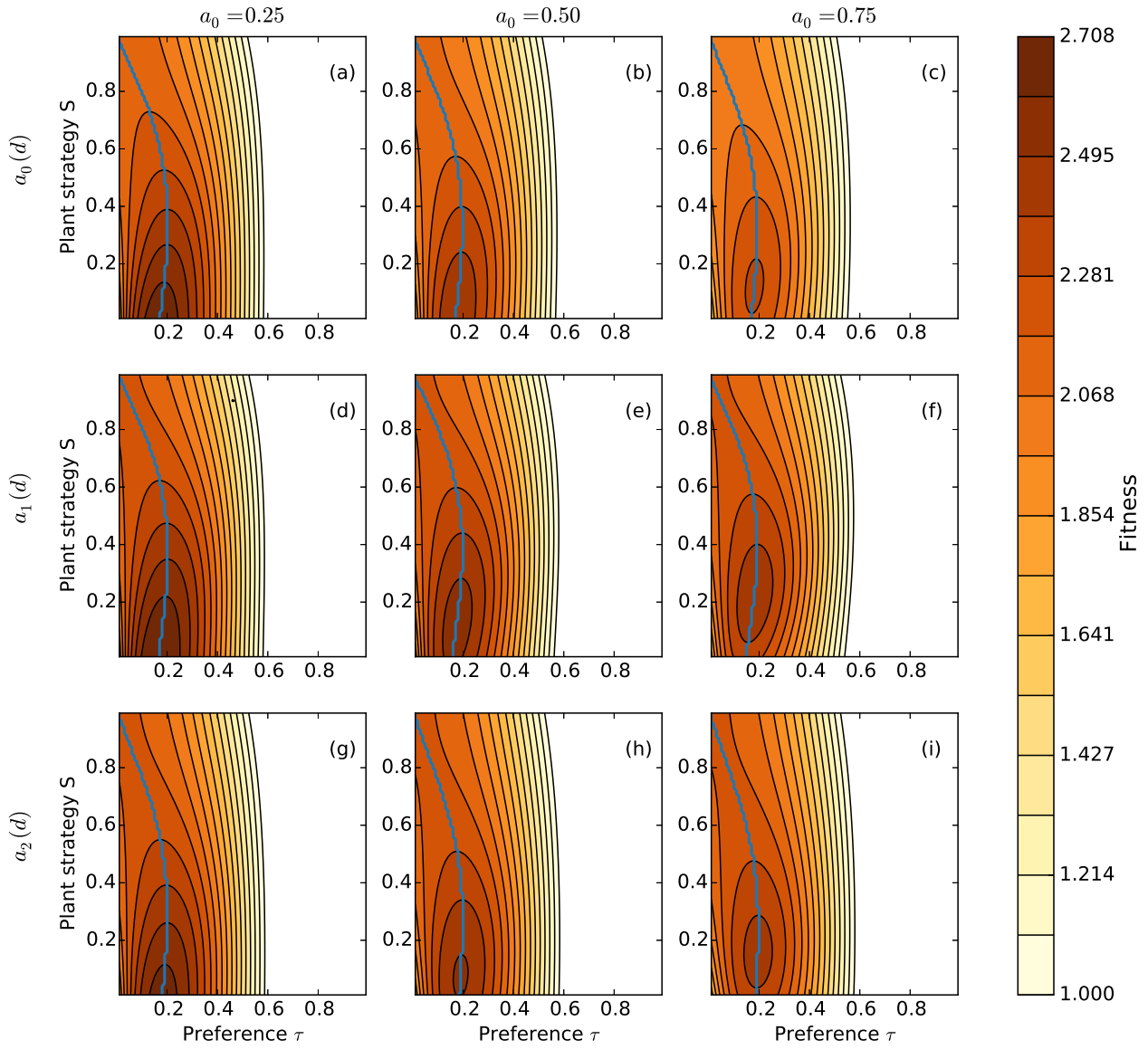

Figure G.5.: Mean fitness (cp. Eq.(5.41)) of a sequestering specialist population in response to the plant strategy parameter S (cp. Eq.(5.5)) and herbivore preference τ (cp. Eq.(5.9)) assuming different functional forms of the probability to be consumed by a predator $a(d)$ (cp. Fig. (G.3)). The predator encounter rate a_0 increases from the left to the right panels.

G.3 Efficiency of converting plant defense

Here, we test the robustness of the fitness landscape of the sequestering specialist in response to changes of the efficiency of converting plant defense θ_S (cp. Eq.(5.39)).

Fig. G.6 shows the fitness $W_H(d)$ (cp. Eq.(5.38)) of a sequestering specialist individual that feeds on a leaf with defense level d for different values of the efficiency of converting plant defense θ_S (cp. Eq.(5.39)). The higher the efficiency of converting plant defense θ_S, the higher is the benefit of the sequestering specialist that feeds on weakly or medium-defended leaves.

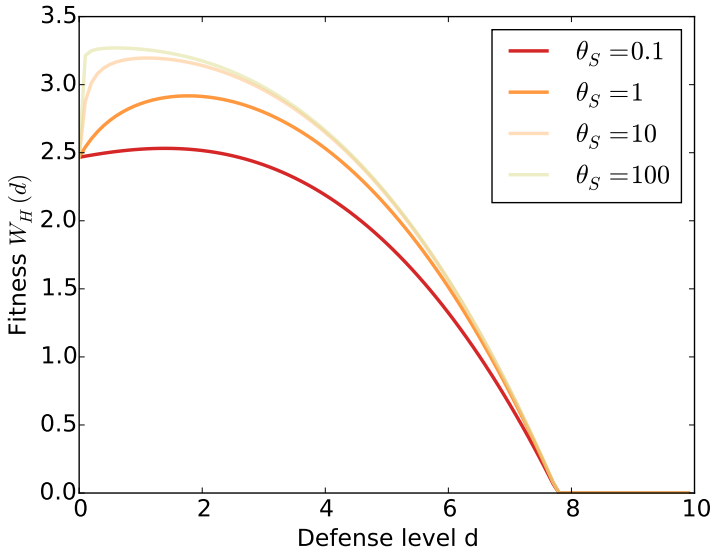

Figure G.6.: Fitness $W_H(d)$ (cp. Eq.(5.38)) of a sequestering specialist individual that feeds on a leaf with defense level d assuming different values of the efficiency of converting plant defense θ_S (cp. Eq.(5.39)).

Fig. G.7 shows the mean fitness of a sequestering specialist population for different values of the efficiency of converting plant defense θ_S (cp. Eq.(5.39)) and in response to the plant strategy parameter S and herbivore preference τ. In the left panels, we use a predator encounter rate of $a_0 = 0.25$, in the right panels, $a_0 = 0.75$.

The efficiency of converting plant defense θ_S only has a slight quantitative impact on the fitness landscape of the sequestering specialist. The reason is that the fitness $W_H(d)$ (cp. Eq.(5.38)) of a sequestering specialist individual that feeds on a leaf with defense level d only changes severely for weakly defended leaves, but as is it not worth to show high preference, these changes have only a slight impact on the fitness landscape. Consequently, the mean fitness changes most when the plant strategy parameter S is low as preference has, in this case, the largest impact (cp. Fig. 5.2(c), (d)). As the efficiency of converting plant defense θ_S only changes the fitness $W_H(d)$ (cp. Eq.(5.38)) of a sequestering specialist individual that feeds on a leaf with defense level d quantitatively, the mean fitness is also only quantitatively affected.

We conclude that the results are robust under changes of the efficiency of converting plant defense θ_S.

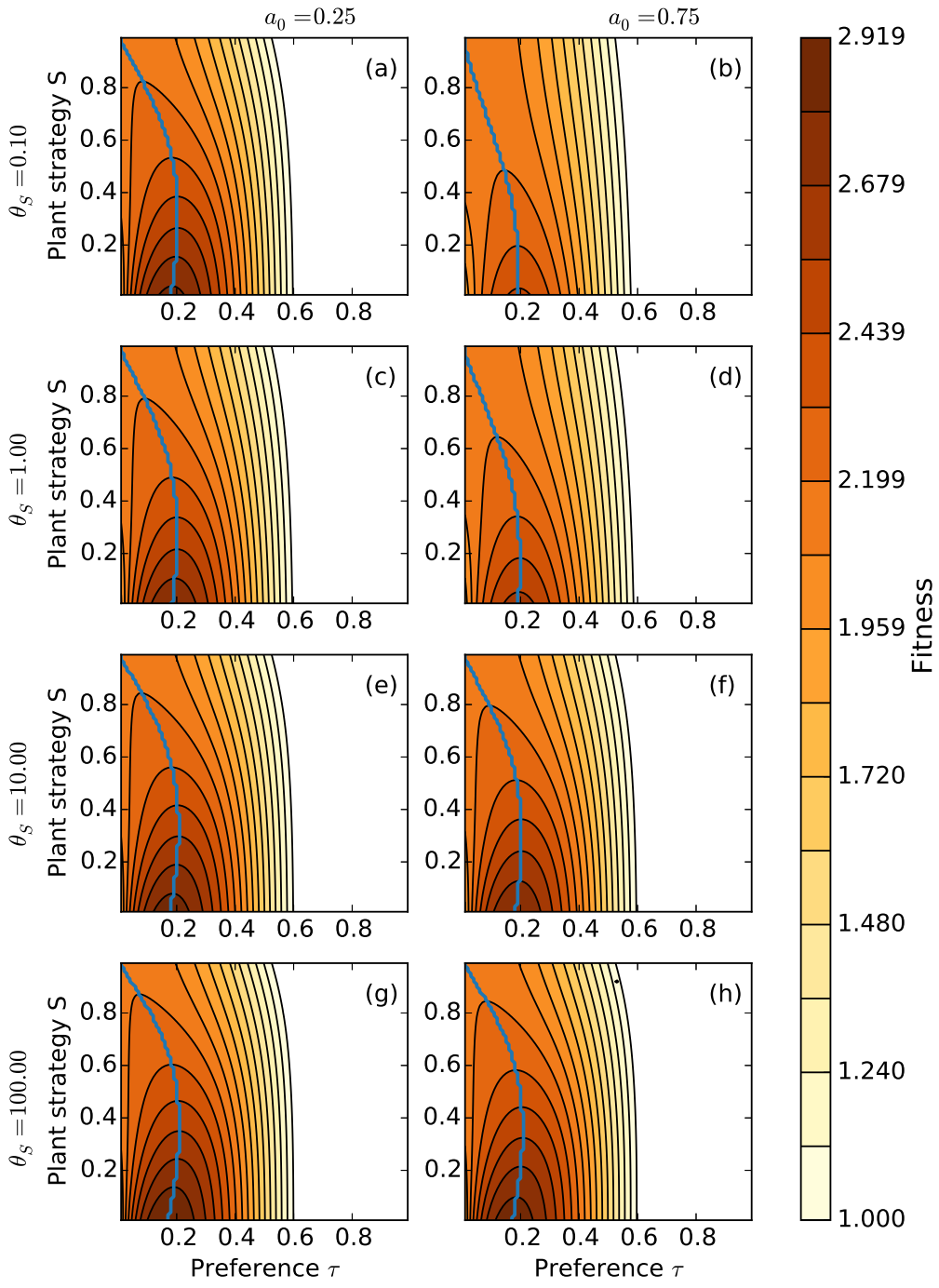

Figure G.7.: Mean fitness (cp. Eq.(5.41)) of a sequestering specialist population in response to the plant strategy parameter S (cp. Eq.(5.5)) and herbivore preference τ (cp. Eq.(5.9)) assuming different values of the efficiency of converting plant defense θ_S (cp. Eq.(5.39)). In the left panels, we use a predator encounter rate of $a_0 = 0.25$, in the right panels, $a_0 = 0.75$.

H Coexistence of plants and herbivores

When the maximal herbivore population, that can coexist, is limited by the available plant biomass because of limited food or place for oviposition, we expect that the herbivore may benefit from other situations. For instance, the benefit of a higher plant biomass may outweigh the fitness loss due to unfavorable conditions for the herbivore.

In order to investigate this, we use a similar approach as in (Gaschler, 2019). Indeed, the extensions to the basic model (s. Section 5.3) used in this section were developed by Sarah Gaschler and Barbara Drossel. Furthermore, Sarah Gaschler found the parameter values that are based on empirical values. The author of this thesis applied this model to investigate the impacts of the plant strategy parameter S and herbivore preference τ on herbivore density and plant biomass.

We assume a logistic growth of the plant biomass M with a growth rate r and a carrying capacity K_P. Furthermore, the plant suffers loss due to herbivory with a herbivore feeding rate a. The herbivore population grows according to its mean fitness $\overline{W}_H$, but is limited by the plant biomass $M(t)$. In terms of equations, this means

$$\begin{aligned} M(t+1) &= M(t) + rM(t)\left(1 - \frac{M(t)}{K_P}\right) - aH(t), \\ H(t+1) &= \overline{W}_H H(t) e^{-H(t)/(K_H M(t))}, \end{aligned} \tag{H.1}$$

where the herbivore limitation factor K_H limits herbivore density per plant biomass.

The parameter values that we used for the growth rate r and the carrying capacity of plant biomass K_P are listed in Tab. H.1 and are motivated by empirical values (Gaschler, 2019). Furthermore, we use the concave downwards performance function f_{neg} shown in Fig. 5.4 for this investigation. When the herbivore population is not limited by plant biomass, we would thus expect that a herbivore population with low preference benefits from low nutrient level variability, but suffers from this situation when having strong preference (cp. Fig. 5.6(c)).

Table H.1.: Parameters used to model the coexistence of plant and herbivore.

Growth rate	Carrying capacity of plant biomass
r	K_P
1.25	100

Fig. H.1 shows the plant biomass and the herbivore population at the stable fixed point in dependency of the plant strategy parameter S and herbivore preference τ. From the top to the bottom row, we increase the herbivore limitation factor K_H.

When the herbivore limitation factor K_H is small (cp. Fig. H.1(a), (b)), the herbivore population shows a similar behavior as in Fig. 5.6(c) – a herbivore population that has low preference benefits from low nutrient level variability, but suffers from this situation when having strong preference. The plant mass shows the contrary trend, i.e. the plant mass increases when the herbivore population decreases. In this case the plant mass is high since the herbivore population is small due to the low herbivore limitation factor K_H. Consequently, the herbivore is not limited by plant mass.

However, the higher the herbivore limitation factor K_H, and thus the higher the plant loss due to herbivory, the higher is the herbivore benefit of a plant strategy parameter S and a herbivore preference τ that allow high plant biomasses. This means that both plant and herbivore population benefit from high nutrient level variability (i.e. low S) when the herbivore has low preference as illustrated by the color change from lighter to darker color with decreasing S. The opposite is true when the herbivore has high preference. The decreased loss due to herbivore limitation thus outweighs the fitness decrease due to less favorable conditions for the herbivore.

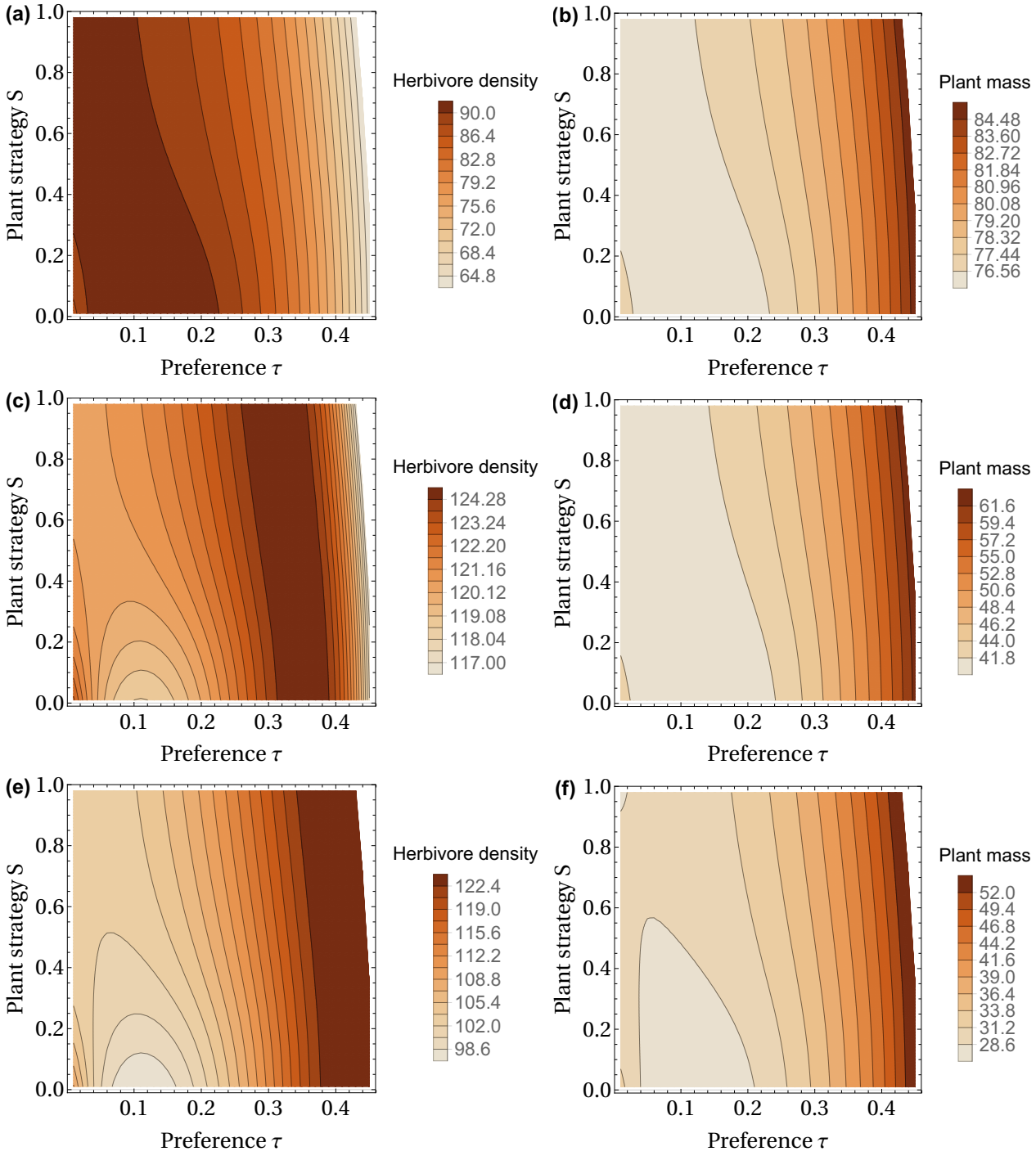

Figure H.1.: Herbivore population and plant biomass on the stable fixed point in dependency of the plant strategy parameter S and herbivore preference τ. The panels differ in the used herbivore limitation factor K_H. In (a), (b) we used $K_H = 1$, in (c), (d) $K_H = 2.5$, and in (e), (f) $K_H = 3$.

Curriculum Vitae

2016 - 2019 **Ph.D. in the group of B. Drossel, Physics** Technische Universität Darmstadt
Migrate, defend, and evolve: Theoretical ecology presented in three different ways

2014 - 2016 **Master of Science, Physics** Technische Universität Darmstadt
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Supervised master thesis

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Supervised bachelor theses

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2017 **Esra Bauer**
Skalengesetze in Räuber-Beute-Systemen

2015 - 2016 **Christian Hoch** (Hoch, 2016)
Robustheit von Nahrungsnetzen im AFK- und Nischenmodell

Teaching

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Komplexe dynamische Systeme

SS 18 **Seminar assistant** AG Drossel
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SS 17 **Tutorial coordinator** AG Feile
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Publications

2019 **Tatjana Thiel, Sarah Gaschler, Karsten Mody, Nico Blüthgen, Barbara Drossel** Oikos
Per se impact of plant defense level variability on specialist and generalist herbivores
Under review (Thiel et al., 2019b)

2019 **Tatjana Thiel, Sarah Gaschler, Karsten Mody, Nico Blüthgen, Barbara Drossel** Theoretical Ecology
Impact of herbivore preference on the benefit of plant trait variability
Under review (Thiel et al., 2019a)

2018 **Tatjana Thiel, Andreas Brechtel, Adrian Brückner, Michael Heethoff, Barbara Drossel**
The effect of reservoir-based chemical defense on predator-prey dynamics Theoretical Ecology
(Thiel et al., 2018)

2018 **Tatjana Thiel, Barbara Drossel** Journal of Theoretical Biology
Impact of stochastic migration on species diversity in meta-food webs consisting of several patches
(Thiel and Drossel, 2018)

Conference Contributions

Talks

2018 **Influence of plant defense level variation on the fitness of specialist and generalist herbivores**
BES Conference, Birmingham

2018 **How does reducible defense alter predator-prey dynamics?** DPG Conference, Berlin

2017 **Impact of Stochastic Migration on Species Diversity in Meta-Foodwebs** DPG Conference, Dresden

2016 **Species Diversity in Coupled Habitats: Going Beyond Homogeneous and Deterministic Models**
MPDE, Marseille

Poster

2017 **Impact of stochastic migration on species diversity in meta food webs consisting of several patches**
3rd Symposium on Ecological Networks and Molecular Analysis of Trophic Interactions, Uppsala

2016 **Species Diversity in Meta-Foodwebs Consisting of Several Patches Coupled by Stochastic Migration**
DPG Conference, Regensburg

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